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THE INFERIOR OLIVE IN VERTEBRATES

ACADEMISCH PROEFSCHRIFT TER
VERKRIJGING VAN DEN GRAAD VAN DOCTOR
IN DE GENEESKUNDE AAN DE UNIVERSITEIT
TE GRONINGEN, OP GEZAG VAN DEN
RECTOR-MAGNIFICUS DR. C. VAN WISSELINGH,
HOOGLEERAAR IN DE FACULTEIT DER WIS- EN
NATUURKUNDE, TEGEN DE BEDENKINGEN DER
FACULTEIT, IN HET OPENBAAR TE VERDEDIGEN
OP VRIJDAG 22 DECEMBER 1916 DES NAMID-
DAGS OM 4 UUR, DOOR FRANS HIERONYMUS
KOOY, ARTS, GEBOREN TE GRONINGEN. ◇ ◇



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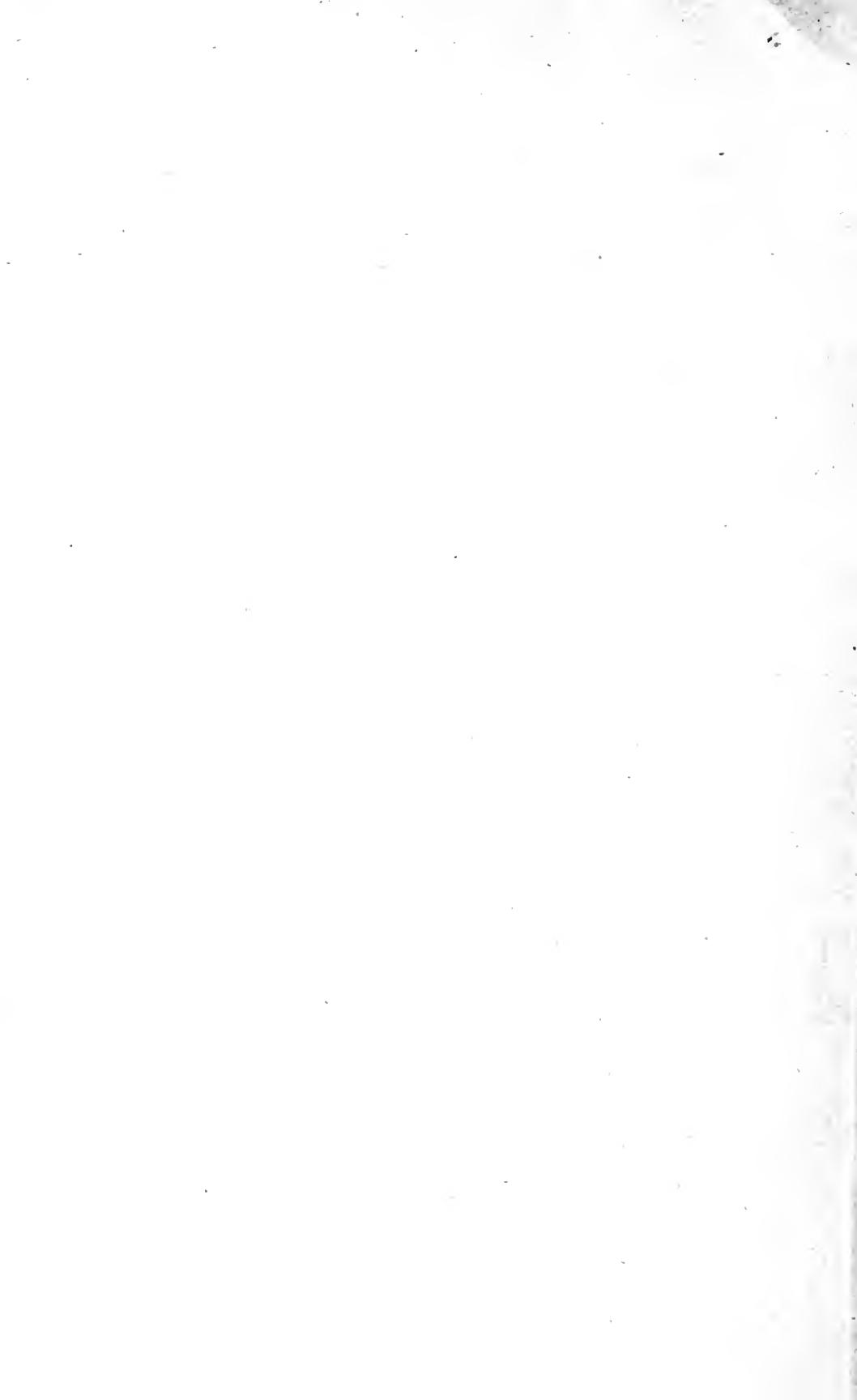
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UNIVERSITY OF CALIFORNIA

HAARLEM — DE ERVEN F. BOHN — 1916.



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AAN MIJN VADER.

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Het is mij aangenaam U, Hoogleeraren, Lector en Privaatdocenten der medische en natuurphilosophische faculteiten, openlijk dank te kunnen zeggen voor het van U ontvangen onderwijs.

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Instituut voor Hersenonderzoek.

Introduction.

The following is a phylogenetic and ontogenetic study of the inferior olive in Vertebrates.

I principally studied the form in serial sections and by making many wax-reconstructions.

The anatomy of the tracts, which have to be considered for a connection with the olive, is not discussed in this paper. I hope afterwards to study them, as it is impossible to understand the differences between the various olives in Vertebrates without considering the tracts. The histology of Fishes and Birds I described in more detail, that is to say, as well as I could without silverstain. The histology of the olive in Mammals, where we have the excellent descriptions of Cajal, is only mentioned by the way.

By the *oliva inferior* of Fishes and Birds, the nucleus is meant, which corresponds topographically to the lower olive of Mammals; to what degree this analogy is correct, will afterwards be discussed.

I made wax-reconstructions of the olive of some Fishes and of nearly all orders of Birds and Mammals¹).

The wax-reconstructions, which Miss Sabin (1901) and L. Weed (1914) made of the nucleus *olivaris inferior*, were so suggestive as to induce me to trace the phylogenetic and ontogenetic development of

Note 1: The olive of Amphibia and Reptiles is too little circumscribed to be drawn or reconstructed.

the olive by this method. Also tables, representing an abbreviated order of sections through the olive are added to my descriptions. In the tables of the mammalian olives, the medial olive is indicated by fine dots, the dorsal one is in solid black, whereas the ventro-lateral (or principal) olive is left white.

The medial part of the dorsal lamella in Birds is indicated by fine dots, its lateral part is darkly dotted, whereas the ventral lamella is left white. The reticular nucleus in all groups is indicated by crosses.

Indistinct places are shown by thin broken lines. In the drawings of the wax-models, the raphe and the ventral border of the bulb, when not reconstructed, are often indicated by dot and dash lines.

In the tables and descriptions I have always supposed the olive to be examined from caudally to frontally. So the most caudal section was numbered 1, and as the other sections, which have been drawn, bear their own original number, the length of each olive-part can be read from the tables. In the wax-models the caudal and the frontal ends are indicated by the letters: C and F.

I shall first discuss the various orders and suborders casuistically with the help of the wax-models and the tables, while at the end of the chapter on Fishes, on Birds and on Mammals, I shall always summarize the morphology and histology.

Moreover a chapter on the *oliva inferior* in Man is added to my phylogenetic descriptions.

The general conclusions on the inferior olive in Vertebrates will be given at the end.

CHAPTER I.

Fishes.

Morphology.

I first intend to describe casuistically the olives of the various Fishes I examined.

I studied the following species (classification Bridge, 1910).

Of Aceratiota¹⁾:

Branchiostoma lanceolatum (Pall) or Amphioxus.

Of Cyclostomata¹⁾:

Petromyzon marinus L.

Bdellostoma dombey (Lacép.)

Myxine glutinosa L.

Of Subclass 1: Elasmobranchii, Order A, Plagiostomi, Suborder 1, Selachi, I examined:

Selache maxima Gunner.

Heptanchus cinereus (Cuv.)

Hexanchus griseus (Cuv.)

Spinax niger Bonaparte.

Scyllium canicula (L.)

Acanthias vulgaris (Riss.)

Note 1: Though these groups do not belong to the Fishes, I have discussed them in this chapter, because too little of their olives can be said, to discuss them in a separate chapter.

Of Suborder 2, Batoidei:

- Raja clavata L.*
Raja circularis Couch.
Torpedo marmorata L.

Of Order B, Holocephala:

- Chimaera monstrosa L.*

Of Subclass 2, Teleostomi, Order A, Crossopterygii:

- Polypterus bichir Geoff.* and
Calamoichthys calabaricus (J. A. Smith).

Of Order B, Chondrostei:

- Acipenser ruthenus L.* and
Polyodon folium Lacép.

Of Order D, Teleostei, I examined a large series of representatives, of which I only mention the following:

- Belone belone (L.)*
Anguilla anguilla (L.)
Alburnus alburnus (L.)
Clupea harengus L.

Of Subclass 3, Dipnoi, I examined:

- Neoceratodus forsteri Kressl.*
Protopterus annectens (Owen).

A m p h i o x u s.

With *Amphioxus* no olive is to be found.

Among **Cyclostomata**, the same can be said about the Myxinidae: *Myxine glutinosa* and *Bdellostoma*, where no trace of it is to be seen.

Concerning *Petromyzon*, I find only one information by J. B. Johnston (1902)¹⁾: "the lower olive presents about the same appearance in *Petromyzon* as in *Acipenser*, but is smaller. It consists of a group of spindle-shaped cells surrounding the roots of the hypoglossus".

Note 1: D. Tretjakoff (1909) disputes Johnston's assertion. He dares not positively interpret the spino-occipital nerve, which Johnston calls hypoglossus, as such. Moreover he says: „Ich finde hier übrigens im Unterschiede von J., nicht spindelförmige Zellen, sondern birnförmige Zellen, und nicht neben den n.n. spino occipitales, sondern höher am lateralen Gehirnrande.“ He attributes these differences to the fact, that Johnston examined an other species and an adult specimen.

I add to this description the drawing of a transverse section (fig. 1), in which at the same level we find some cells, which partly correspond

to Johnston's description, partly are more angular (fig. 2). Moreover, I do not find the cells surrounding

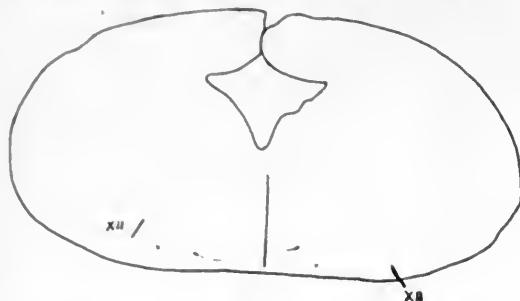


Fig. 1.
Transverse section through the medulla oblongata
of *Petromyzon marinus L.*

the hypoglossus, but lying for the greater part medially of it.

In sagittal and horizontal sections, I could not discern the olive with certainty. Its boundaries are so indistinct, that I find it impossible to make out its form.

Fig. 2.
Cells of the olive in *Petromyzon marinus L.*

Plagiostomi.

Selachi. I only find some informations by Edinger (1908), Kappers (1906) and Sterzi (1909).

They all give a drawing of a transverse section, in which the so-called "nucleus paraseptalis" is to be seen; moreover Sterzi reproduces a sagittal section of Acanthias. I made an analogous drawing of the olive of *Scyllium canicula* (L.), fig. 3.

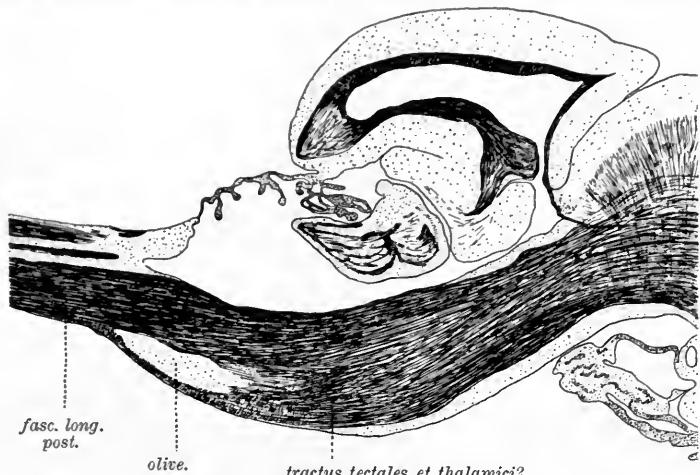


Fig. 3.
Scyllium canicula (L.) — Sagittal — 7.5 ×.

My own researches concern several representatives of this class.

I shall start my descriptions with *Selache maxima*, because the olive of this animal was the most suitable for a reconstruction.

Selache maxima Gunner — Wax-reconstruction: fig. 4, Table 1.

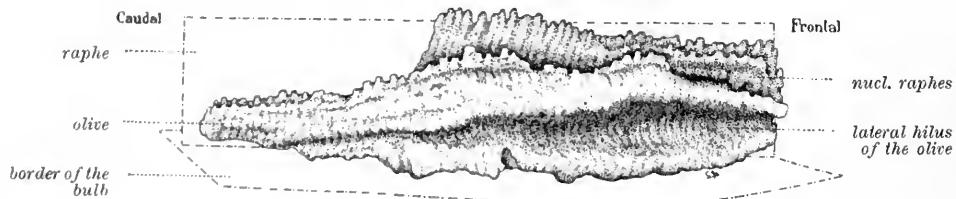


Fig. 4.
Inferior olive of *Selache maxima Gunner* — 10 X.

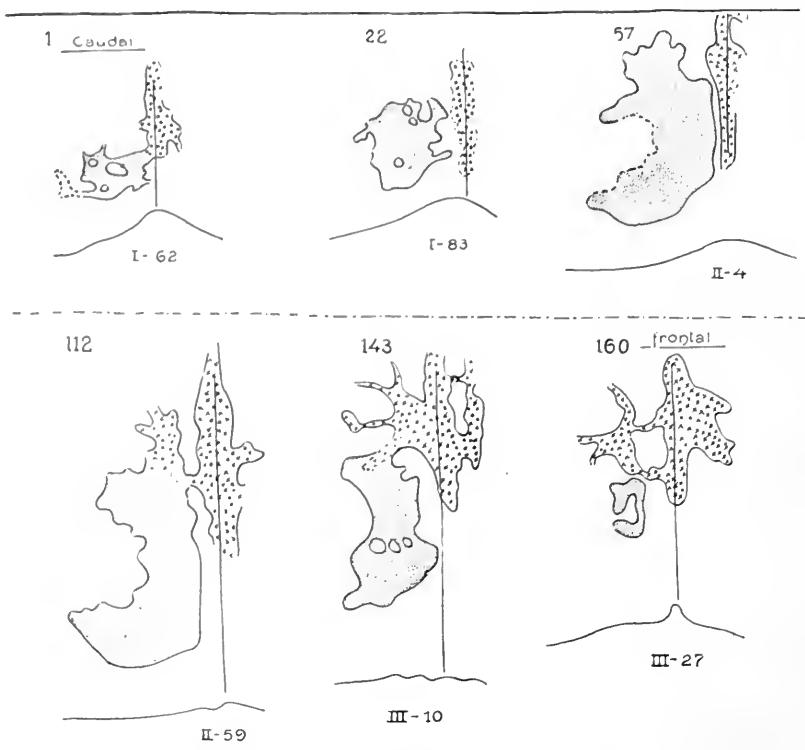


Table 1.
Abbreviated order of sections through the inferior olive of
Selache maxima Gunner.

Size of the sections 1—22 = 50 μ .

57—160 = 60 μ .

Magnified 20 X.

As is the case with all Fishes, the olive is oblong (length $9120\mu^1$, greatest heighth 1550μ , greatest breadth 750μ), and situated in its full length beside the raphe; for the greater part it shows a hilus at its lateral side and does not reach far laterally, neither in frontal, nor in caudal regions.

Between the two olives, along their frontal threequarter part, a nucleus of large reticular cells is situated in the raphe (indicated by crosses in the table).

At the frontal top of the olive it is still present in its full size.

Histology.

Viault gave already in 1870 this very accurate description of the olive-cells in Plagiostomata:

„Elle se compose de très petites cellules nerveuses piriformes, plongées dans une substance granuleuse assez analogue à celle du cervelet et très riche en vaisseaux capillaires.”

I have little to add to this, I also find the olive-cells pear- and



Fig. 5.

Cells of the olive in *Selache maxima* Gunner — 196 ×.

spindle-shaped, with often visible fine dendrites (fig. 5). I considered them to be the specific cells, because they are present throughout the whole olive-region and do not occur outside it. The reticular cells are for the greater part situated in the grey substance of the raphe (subst. grisea sagittal-Sterzi) and between the fasciculi longitudinales posteriores. Along the caudal part of the olive we find only small (glia?) cells, situated between the two olives.

A little before the middle of the olive, big cells appear (fig. 6), which do not extend dorsally between the f.l.p.'s, but remain compact at the dorsal top of the olives (quite near the raphe, often perpendicular on it). More frontally, a cell or its dendrites often stretch dorsally round the olive, or enter into it.

So, though there really is a distinct difference in the frontal and the caudal sections, I reconstructed and drew this body as a whole, because of the gradual

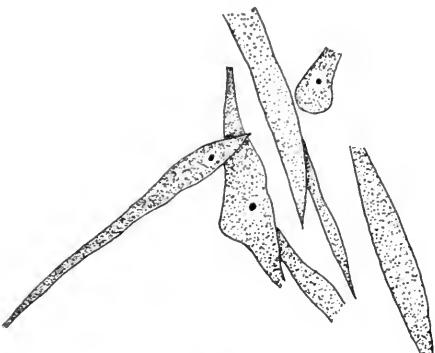


Fig. 6.
Reticular cells of the raphe in *Selache maxima* Gunner — 196 ×.

Note 1: The olive is presumably a little longer; this, however, cannot be reconstructed.

transition, and as the smaller cells remain present at the same time with the large cells.

These reticular cells are not described with Selache; Van Hoeyvell (1911) does so with Raja. He divides the reticular cells of the whole bulb into three nuclei, places where they accumulate, while they are united by parts which contain less of these cells.

The lowest of these nuclei, which occupies the vagus-region, is situated in the raphe, but the more scattered cells, laterally in the bulb, are also considered by him to belong to these.

I cannot say whether these lateral cells have any connection with the medial ones, but it is certain that also in the nucleus reticularis of the vagus-region in Raja, the accumulation in the raphe is rather circumscribed. It is difficult to decide whether these cells have anything to do with the olive, as it is always hard to ascertain the connection of these scattered cells in general.

They are probably of many kinds (Cajal, Literature, 4—1909).

It is, however, striking, that frontally of the olive, the raphe-nucleus becomes less circumscribed and the number of the reticular cells in the rest of the bulb increases, so that the raphe nucleus seems to be no longer kept together and to be loosened over a larger region.

Lastly, one sees in several sections the dendrites of the reticular cells penetrate into the olive.

Microscopical research of the other plagiostomata.

Heptanchus and *Hexanchus* offer nothing particular in their forms; they both resemble Spinax. I have no opinion on the cell-type of these fishes, because I have only series in Weigert-stain.

Spinax niger Bonap.

The form and dimensions are similar to those of Selache, though there is no hilus and its height is less. The olive-cells are small and spindle-shaped (fig. 7); the reticular elements are distinct, though not accumulated to a compact nucleus in the raphe, on the contrary, their greatest number on the level



Fig. 7.

Cells of the olive in *Spinax niger Bonaparte* — 196 ×.

of the olive can be found in the ventrolateral border of the bulb.



Fig. 8.

Cells of the olive in *Scyllium canicula (L.)*
196 ×.

Scyllium canicula (L.).

The olive in *Scyllium* resembles that in *Spinax* very much. Its

cells, though still of the spindle-shaped type, are nearly round (fig. 8).

The reticular elements, of which I cannot find a special grouping on this level, are oblong-spindle-shaped, sometimes a little angular.

Batoïdes.

Also several representatives of the Batoïdes were examined. Wax-reconstructions were made of *Raja clavata* L. and *Raja circularis* Couch.

Raja clavata L. — Waxreconstruction: fig. 9, Table 2.

Here the olive is for the first time no longer undivided. Wax-

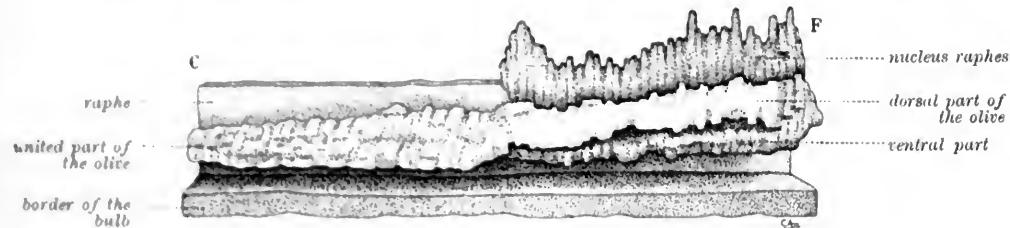


Fig. 9.
Inferior olive of *Raja clavata* L. — 14.5 ×.

reconstruction 2 (fig. 9) shows how it lies over its caudal half as a whole near the raphe; over its frontal half, however, it is divided into a ventral and a dorsal part, while both parts diverge



Fig. 10.

Cells of the olive in
Raja clavata L.
196 ×.

a little from the raphe. In the latter a reticular nucleus lies along the frontal part of the olive.

Histology: The cell-type is spindle-shaped (fig. 10); the reticular cells are exactly like those in Selache (fig. 11).

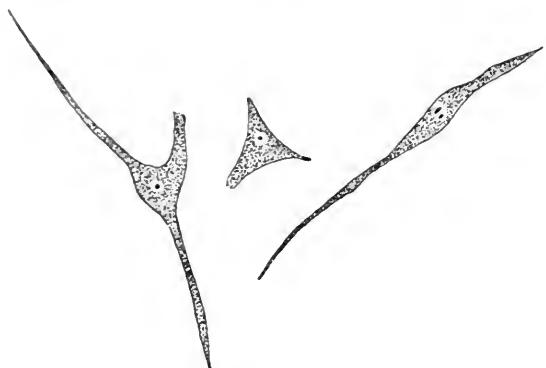


Fig. 11.
Reticular cells of the raphe in *Raja clavata* L.
196 ×.

Raja circularis Couch. — Waxreconstruction: fig. 12, Table 3.

The olive of this ray is very much like that of *Raja clavata*; its

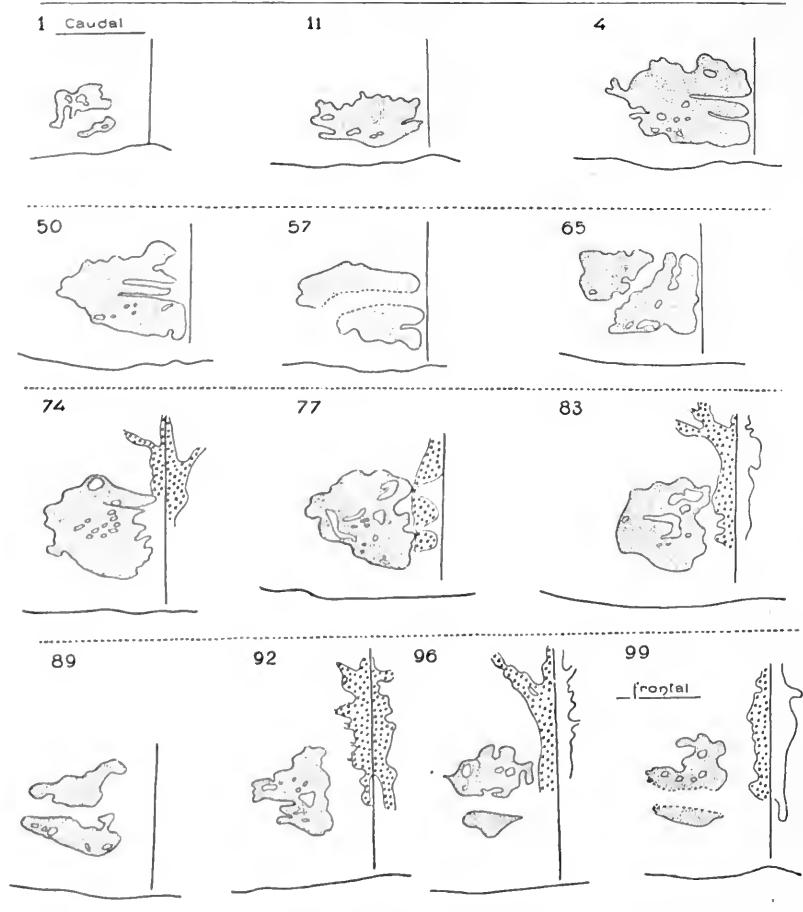


Table 2.
Abbreviated order of sections through the inferior olive of
Raja clavata L.

Size of the section = 50 μ .

Magnified 21 X.

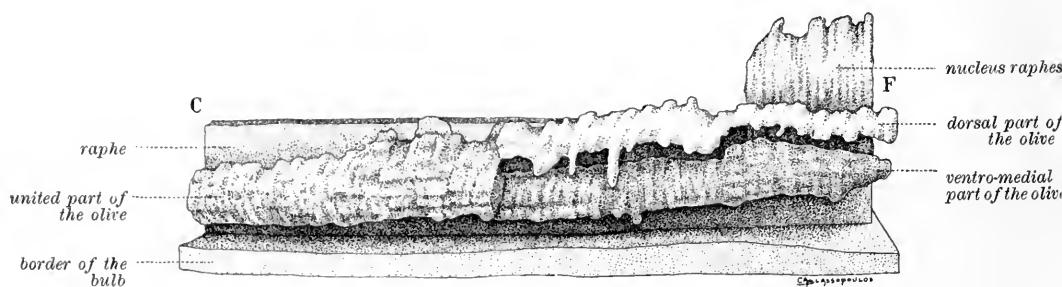


Fig. 12.
Inferior olive of *Raja circularis* Couch — 14.5 X.

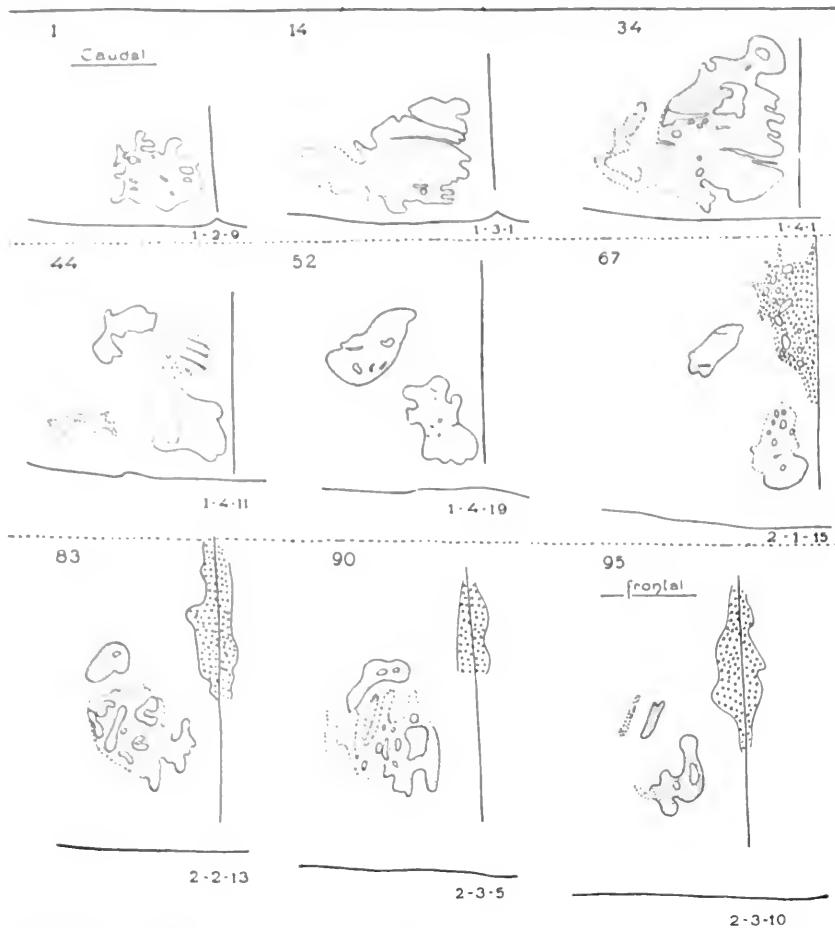


Table 3.
Abbreviated order of sections through the inferior olive of
Raja circularis Couch.

Size of the section = 60 μ .

Magnified 21 \times .



Medial part.



Dorsal part.

Fig. 13.

Cells of the olive in *Raja circularis* Couch
196 \times .



Fig. 14.

Large cells at the lateral border of the bulb
in *Raja circularis* Couch — 196 \times .

parts are still more distinctly separated, the dorsal one of which is most circumscript¹⁾; it is moreover situated in a plane, which makes an angle of 45° with the raphe.

The reticular nucleus reaches less caudally than in *Raja clavata*.

Histology: see figs. 13 and 14.

Torpedo marmorata (L.).

I have no opinion on the form, as I have only a series in cell-stain.



Fig. 15.

Cells of the olive in
Torpedo marmorata (L.)

196 X.

The cells are smaller and more spindle-shaped (fig. 15); in sections through the frontal top of the olive, the raphe contains reticular elements.

Situation and type of those cells are quite analogous with those of *Selache*, though in *Torpedo* they are also numerous in the rest of the bulb.

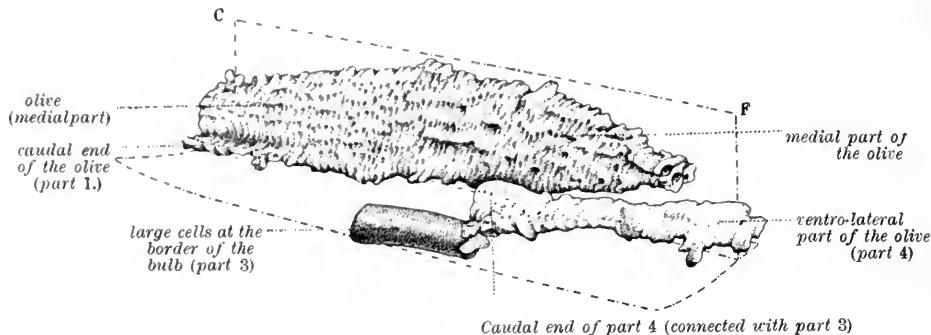
Moreover, frontally of the olive, the raphe nucleus remains for some time equally compact, as contrasted with that of *Selache*.

Holocephala.

Chimaera monstrosa L. — Wax-reconstruction: fig. 16, Table 4.

The structure of the olive and its surroundings, like the rest of the nervous system, is a transition between *Selachi* and *Teleostei*.

The dimensions are almost the same as those of *Selache maxima* (fig. 16);



Inferior olive of *Chimaera monstrosa* L. ± 25 X.

there is also a hilus, but on the medial side, caused by a small tract.

At its caudal end, the olive stretches more laterally than in the middle, but frontally we find a much larger ventro-lateral part. This shows some peculiarities in its cell-type, it is practically free from the

Note 1: Especially the dorsal outline of the ventral part is very indistinct.

rest of the nucleus (the places of connection are very dubious) and extends more frontally than the original part, taking its place in the most frontal sections.

Caudally, it is connected with a group of large cells, which lie at the very outside of the bulb and cause a small protrusion there. In the wax-reconstruction I modelled this latter part in rough outline (Table 4, part 3).

Microscopical research.

With Chimaera one sees caudally two parts in the olive.

The most caudal grey substance is seen ventrally of the complex: fasciculus longitudinalis posterior plus fasciculus praedorsalis (Table 4,

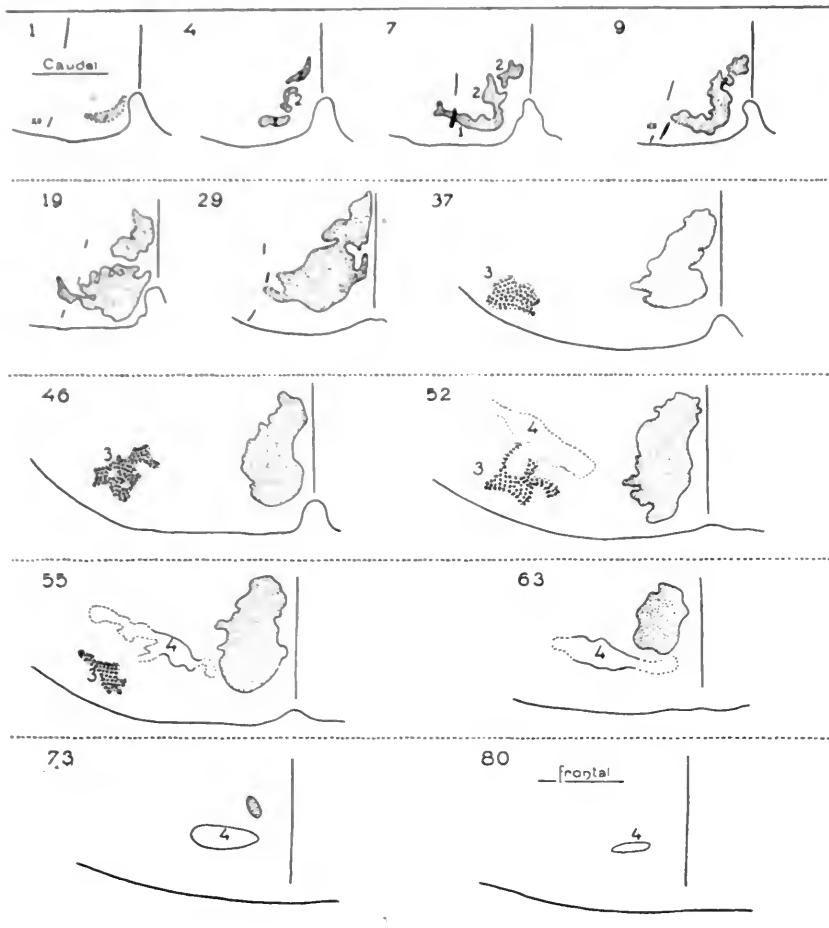


Table 4.

Abbreviated order of sections through the inferior olive of *Chimaera monstrosa L.*

Size of the section = 60 μ .

Magnified 20 \times .

part 1); this part is soon joined by a more dorsal one (Table 4, part 2), appearing among the most ventral fibres of the above-mentioned complex.

By the further development of the olive, these ventral fibres are thronged into a compact small tract beside the raphe, which causes a medial hilus in the olive (Table 4, s. 19 a.s.o.).

In the following sections, the ventral and the dorsal part (parts 1 and 2) become united.

Histology. (figs. 18, 19 and 20).

The caudal cells of part 4 are bigger than those of the medial one (parts 1 and 2), though smaller than the large ones of part 3.

More frontally, however, only a few bigger cells are still to be found,



Fig. 18.
Cells of part 4 in
Chimaera monstrosa
L. — 196 ×.



Fig. 19.
Cells of part 3 in *Chimaera*
monstrosa L. — 196 ×.



Fig. 20.
Cells of the olive (medial
part) in *Chimaera*
monstrosa L. — 196 ×.

whereas the greater part represent the ordinary cell-type. So it is a case of gradual transition. On account of the different cell-type and the peculiar situation, I dare not with certainty classify part 3 as belonging to the olive.

The *reticular* nucleus has been described by Ariëns Kappers (1911), who calls it quite analogous with the raphe-nucleus of the X-region in Raja, mentioned by Van Hoevell: "extending laterally underneath the f.l.p. in the form of a garland; more frontally there are hardly any reticular cells to be found in the raphe".

This resembles the reticular nucleus in Selache and Raja.

I cannot find this nucleus in my specimen of Chimaera. (Kappers used carmine-stain; I had Weigert and Van Gieson-preparations.)

For the olives of the *Crossopterygii*:

Polypterus bichir and

Calamoichthus calabaricus, it will be sufficient to refer to those of Teleostei, as they are so very much alike.

Acipenser ruthenus L.

Johnston (1901) mentions the inferior olive in Acipenser; in silver-preparations the cells are found lying round the hypoglossus.

Caudally of the olive I found complexes of big fibres which reach the raphe from either side, but for a strand of finer fibres.

More frontally, this strand increases and at its lateral side, small

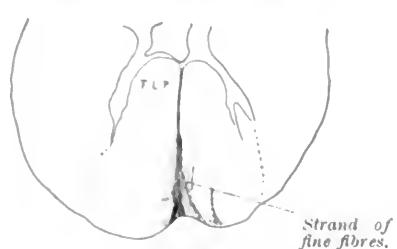


Fig. 21.
Acipenser ruthenus L.
(van Gieson-Stain) — 20×.



Fig. 22.
Acipenser ruthenus L. (van Gieson-Stain) — 20×.

spindle-shaped cells appear, which are undoubtedly the cells, meant by Johnston (figs. 21—23).

Quite the same can be said of:

Polyodon spathula.

Amia calva L. and

Lepidosteus osseus (L.).

In his researches on these animals with the help of silver-stain, Ariëns Kappers (1907) mentions the nucleus paraseptalis and describes its presumable connections. I found, in the Weigert and v. Gieson-preparations of the Institute, only a lighter coloured spot and cannot describe a form or cell-type.

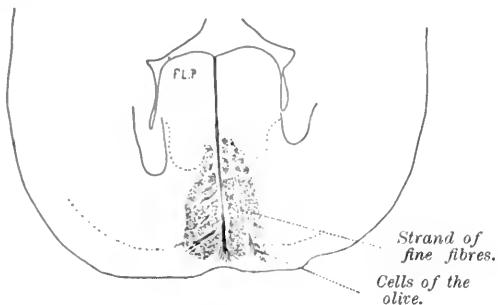


Fig. 23.
Acipenser ruthenus L. (van Gieson-Stain) — 20×.

Teleostei.

The olive in Teleostei is mentioned by only few authors; most of them, however, do not discuss it any further. Others say to have been unable to find it.

Though present in every bone-fish, the olive is indeed not so conspicuous in any Teleost as in Selachians. Before the microscopical techniques was improved, informations were given by: Serres (1824—27), Haller (1898), Carus (1853), Götsche (1835).

Of the later writers, Mayer (1882) describes it as follows: "Die Oliven besitzen zahlreiche kleine Nerven-körper In den darüber liegenden gelatinösen Substanz dagegen, scheinen die Nervenzellen ganz zu fehlen".

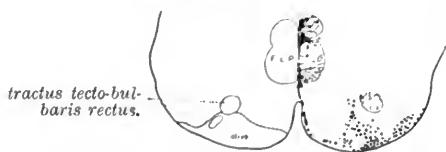


Fig. 24.
Inferior olive of *Clupea harengus L. (juvenilis)*
(23.4 mm).

Haematoxyline-Eosine — 100 X.

Perhaps the latter fact has been the cause of the difficulty, there was in discovering the olive. The form of the olive in Teleosts is indeed entirely different from that in Sharks and Rays, for the cells are only situated along the ventro-lateral border of the bulb (see *Clupea harengus L. juvenilis* fig. 24, wax-reconstruction: fig. 25, and *Alburnus alburnus* (L.), fig. 26).

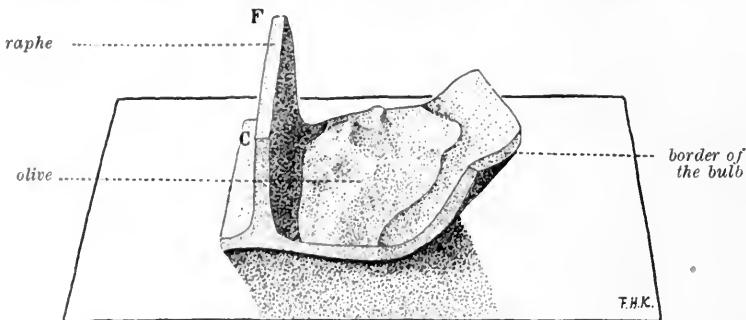


Fig. 25.
Inferior olive of *Clupea harengus L. (juvenilis)* 130 X.

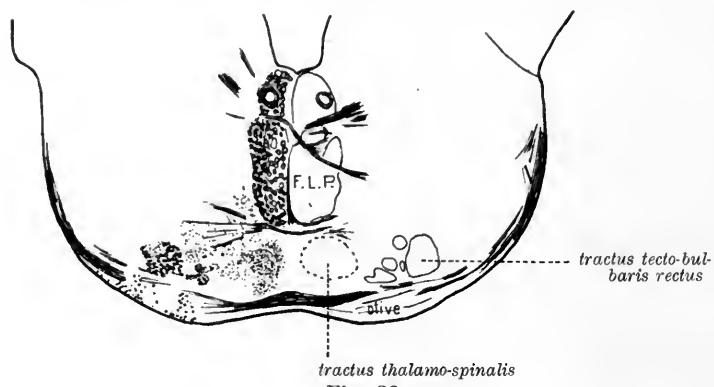


Fig. 26.
Inferior olive of *Alburnus alburnus* (L.) — 40 X.

Dorso-medially of these cells, nearer the raphe, where in Sharks a considerable number of olive-cells occurs, a more or less gelatinous sub-

stance is found, which does not seem to contain any cells at all, but many fine fibres.

Even the few cells of the olive, accumulated at the ventro-lateral border of the bulb, are often hidden by the many fibres and tracts.

Histology:

The very small cells are round, oblong or spindle-shaped (figs. 27 and 28).

I cannot find a reticular nucleus in Teleostei on the level of the olive.



Fig. 27.

Cells of the olive in
Alburnus alburnus (L.)
200 ×.



Fig. 28.

Cells of the olive in *Anguilla*
anguilla (L.) — 200 ×.



Fig. 29.

Cells at the lateral bor-
der of bulb in *Anguilla*
anguilla (L.) — 200 ×.

In *Anguilla anguilla* (L.), like in *Raja* and *Chimaera*, large cells are accumulated on the lateral border of the bulb, medially of the tractus olivo-cerebellaris (fig. 29).

In the *Dipnoi*, which I examined:

Ceratodus forsteri and

Protopterus annectens I could not state the presence of the olive with absolute certainty.

Conclusions.

In Fishes, at the place of transition of spinal cord and medulla oblongata, an accumulation of small cells¹⁾ can be found near the ventral border of the bulb.

In Selachi, Rajidae and partly in Chimaera they lie beside the raphe, in Teleostei and also partly in Chimaera, more laterally. The latter fact may be caused by the lateral position of the tractus tecto-bulbaris rectus, or the above-mentioned substantia gelatinosa may move the olive in a lateral direction. As I have avoided to discuss the tracts in this paper, I cannot enter deeper into the question here.

In Plagiostomata (and Holocephala?), a reticular nucleus occupies the raphe along the frontal half of the olive.

Note 1: If one disregards the large lateral cells of *Raja*, *Chimaera* and *Anguilla*, which probably have nothing to do with the olive.

CHAPTER II.

Birds.

Morphology.

First I intend to describe casuistically the olives of the various birds, I studied.

I examined the following species (Classification of H. Gadow 1898):

Of Division 1, Neornithes, Ratitae:

Casuaris australis Wall.

Of Division 3¹⁾, Neornithes, Carinatae;

Order 2²⁾, Colymbiformis:

Colymbus septentrionalis L.

Podiceps cristatus (L.)

Order 3, Sphenisciformes:

Spheniscus demersus (L.)

Order 5³⁾, Ciconiiformes:

Ciconia ciconia (L.)

Order 6, Anseriformes:

Cygnus olor Gm.

Order 7, Falconiformes:

Cathartes urubu (Vieill.)

Haliaetus melanoleuca (?)

Note 1: Division 2, Neornithes odontolcae, is extinct.

Note 2: Order 1, Ichthyornithes, is extinct.

Note 3: Order 4, Procellariiformes, was not represented in the Institute.

Order 9¹), Galliformes:

Gallus gallus (L.) *domesticus*.

Lophortyx californicus (Shaw & Nodd)

Order 10, Gruiformes:

Grus japonensis (P. L. S. Müll.)

Order 11, Charadriiformes:

Larus argentatus (Gm.)

Columba guinea L.

Columba livia Bonn. (*domestica neon.*)

Order 12, Cuculiformes, Suborder Psittaci:

Cacatua roseicapilla Vieill.

Palaeornis cupatria (L.)

Ara psittacus (?)

Order 13, Coraciiformes:

Athene nocturna (Scop.)

Order 14, Passeriformes (Oscines²):

Sturnus vulgaris L.

Pratincola rubicola (L.)

The olive in Birds has two lamellae, a dorsal and a ventral one, both parallel to the border of the bulb, of which the dorsal lamella is by far the largest.

This holds true with all birds, so that I shall not repeat it in every description.

1. *Casuaris australis* Wall. — Waxreconstruction: fig. 30, Table 5.

The dorsal lamella is thin; over its caudal three-quarter part, it can be divided into a medial and a lateral part, which are connected by thin bridges of a few olive-cells. Frontally, only the medial part remains.

The ventral lamella consists caudally of very few cells (Table 5, section 21—34); it is, therefore, very difficult to outline. I did not reconstruct it and indicated it in the drawings (Table 5) by a broken line. More frontally, its lateral part grows distinct and has an almost round form. The medial part of the ventral lamella, which is connected with the dorsal one, remains very indistinct.

Note 1: of Order 8, Tinnamiformes, I had no specimen.

Note 2: of Pseudoscines (Clamatores) I had no specimen.

Still more frontally, only the medial part of the dorsal lamella and the lateral part of the ventral one, are present.

The following points again hold true with all Birds, but for some insignificant exceptions.

Examining the sections from caudally to frontally (Table 5), the first appearance of the dorsal lamella is seen rather laterally in the

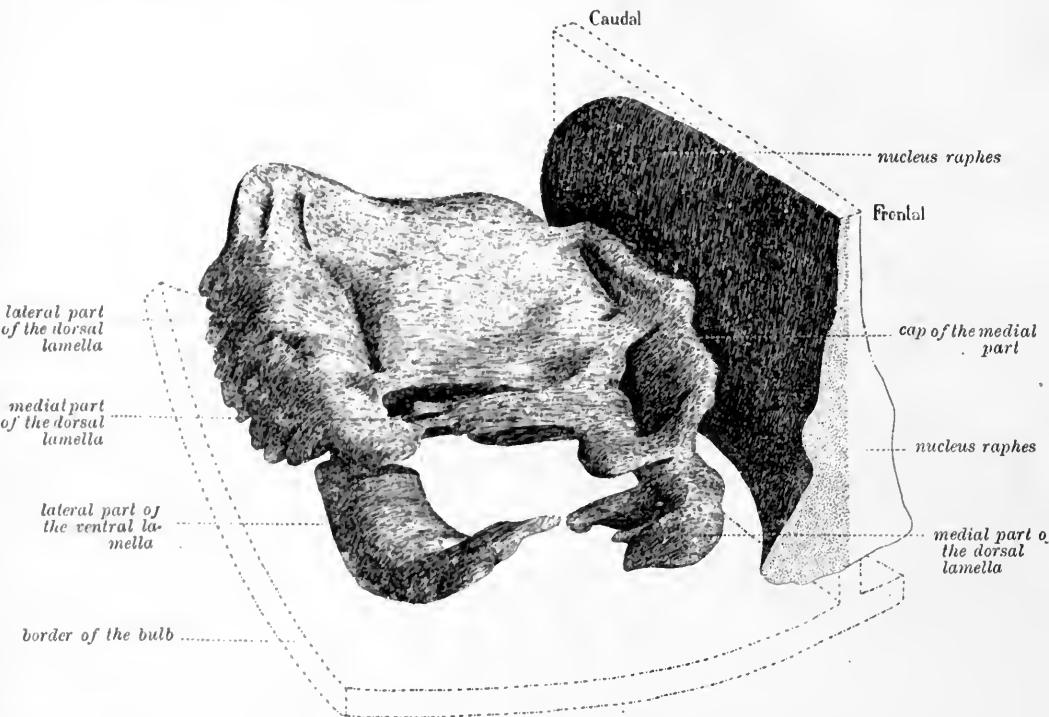


Fig. 30.

Inferior olive of *Casuaris australis* Wall. — 20 X (frontal and dorso-lateral view).

bulb; increasing in the next sections, it reaches unto the raphe and at the same time extends dorso-laterally.

The 12th nerve, leaving the bulb medially of the olive in caudal sections, crosses the medial part on a more frontal level and often makes a little incision or interrupts it.

This is found in all the birds I examined. As it is, however, of no importance to the form or connections of the olive, I shall henceforth not consider the hypoglossus (its position can moreover, be seen in the Tables).

When the olive approaches the raphe, a *reticular nucleus* appears

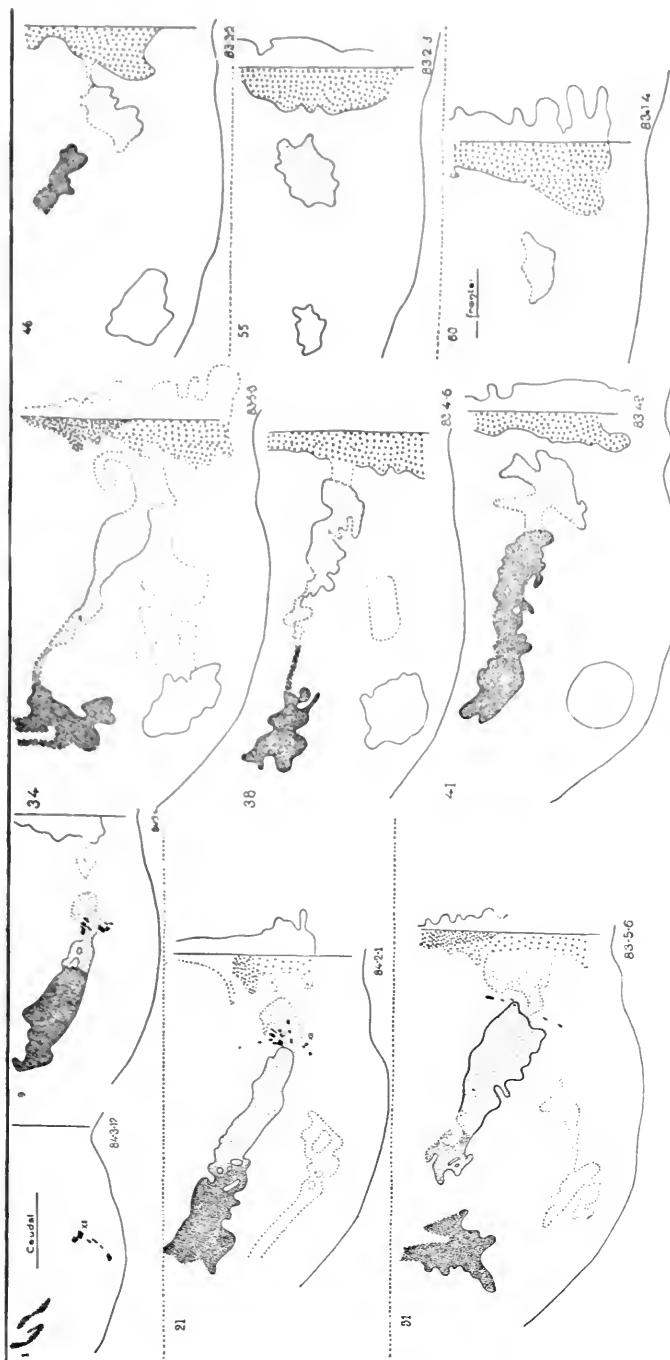


Table 5.
Abbreviated order of sections through the inferior olive of *Casuaris australis* Wall.
Magnified 13.3 X.
Size of the section = 60 μ .

in the latter (see also fig. 30), which increases in a frontal direction (especially in its dorso-ventral dimension).

Between the olive and the reticular nucleus is a strand of fine fibres,

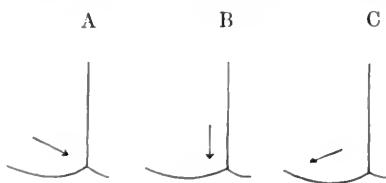


Fig. 31.

Scheme, showing the turning of the medial part of the dorsal lamella.

in which no cells are to be found, and from which it is often difficult, to distinguish the medial part of the olive.

The frontal top of the dorsal lamella can best be seen in fig. 30 and in Table 5, section 38—60; this part namely, turns about 90° (as is represented schematically in

fig. 31) and at the same time, diverges a little from the raphe.

Parts of the olive are sometimes so poorly developed, that misgivings may arise whether they are present or not.

The best example of this is the ventral lamella of the Casuaris-olive. Yoshimura (1910) describes in Ratitae (*Struthio camelus*) a dorsal lamella only, as an exception to the rule of the two-lamellae-system in other Birds. What I described as the distinct part of the ventral lamella, he considers to be a separate lateral cell-accumulation.

The cause of this is doubtless that at several places in all birds some strands of olfactory cells are very indistinct. This is especially the case with the medial part of the ventral lamella, which connects its more distinct lateral part with the dorsal lamella (see Table 5, s. 34; Table 9, s. 44; Table 10, s. 47; Table 11, s. 33; Table 13, s. 18).

Also other places f. i. those between the lateral and the medial part of the dorsal lamella (Table 5, sections 34, 38) are often indistinct.

In all birds, the delimitation is very difficult on frontal levels. Not only because the number of the cells decreases, but also because they are more scattered, so that various parts of the olive cannot easily be distinguished.

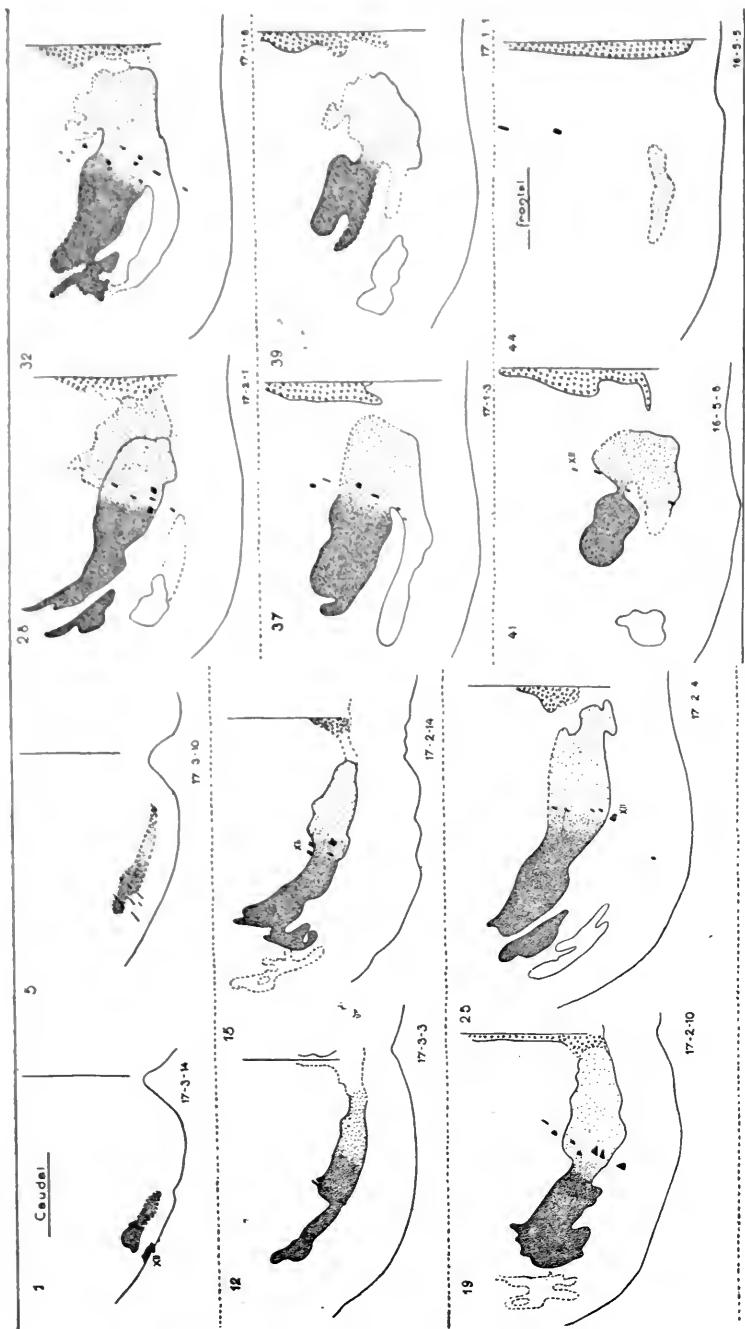


Table 6.
Abbreviated order of sections through the inferior olive of *Colymbus septentrionalis* L.
Magnified 43.3 X.
Size of the section = 60 μ .

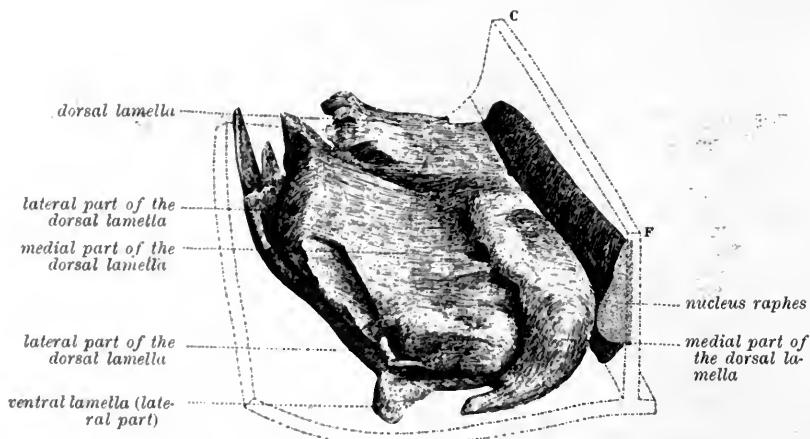


Fig. 32.

Inferior olive of *Colymbus septentrionalis* L. — 17.5 ×
(frontal and dorso-lateral view).

Colymbus septentrionalis L. — Waxreconstruction: fig. 32, Table 6.

The dorsal lamella has the usual flat shape; a division into a medial and a lateral part can only be made in frontal¹⁾ sections.

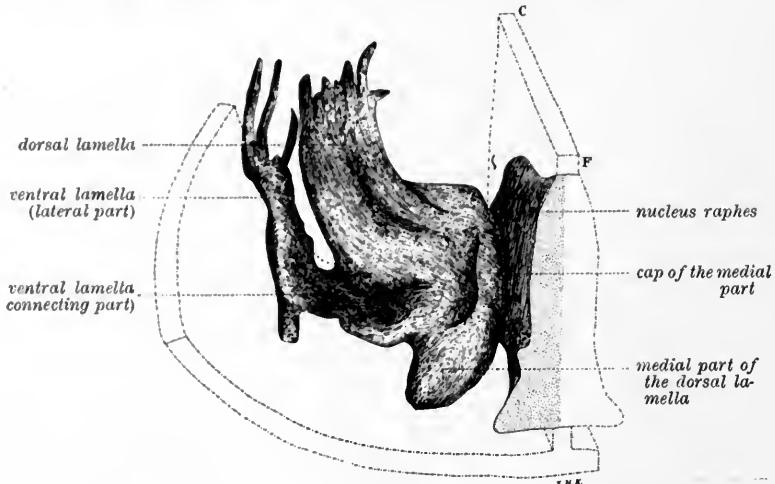


Fig. 33.

Inferior olive of *Podiceps cristatus* (L.) — 18 × (fronto-dorsal view).

On the same level as where the medial part gets a dorsal cap, the lateral one is more or less free and placed perpendicular on it (Table 6, s. 39, 41).

Note 1: With frontal is always meant the opposite of caudal; it is never used in the significance of „transverse”.

Most frontally, only the medial part remains.

The *ventral lamella* has a lateral position on a caudal level, more frontally it is connected with the medial part of the dorsal lamella; thus a hilus is formed, which opens laterally (Table 6, s. 32, 37).

The lateral part of the ventral lamella reaches most frontally.

The *reticular nucleus* presents no particulars.

Podiceps cristatus (L.). — Waxreconstruction: fig. 33, Table 7.

In this bird, the bulb is rather narrow; hence the olive reaches far dorsally on one side, whereas we find, notwithstanding this, the greatest cell-accumulation near the raphe.

A distinct division of the *dorsal lamella* into a medial and a lateral part is impossible.

Near the raphe, it shows a dorsal cap (Table 7, s. 15—22; fig. 33), while in more frontal sections, it turns as described in Casuaris.

The *ventral lamella* is rather short and is connected with the medial part of the dorsal lamella; the middle of

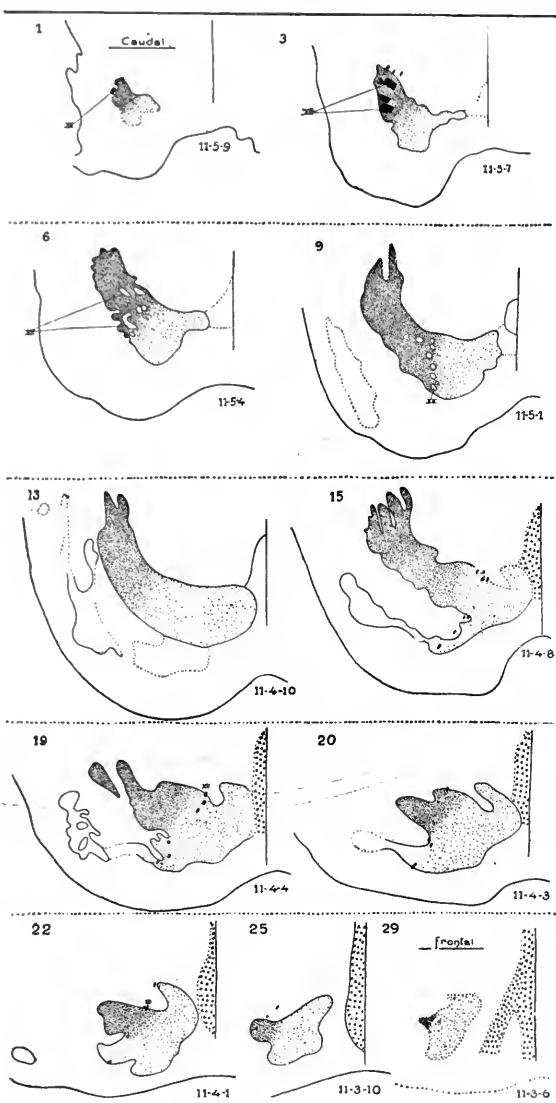


Table 7.
Abbreviated order of sections through the inferior olive
of *Podiceps cristatus* (L.).

Size of the section = 60 μ .

Magnified 13.3 \times .

this connection is rather indistinct and very thin (Table 7, s. 13—19). Its lateral part reaches most frontally.

Frontally, the *reticular nucleus* is cleft at its ventral side (Table 7, s. 29).

Spheniscus demersus (L.). — Waxreconstruction: fig. 34, Table 8.

A division into a lateral and a medial part of the *dorsal lamella* can be made throughout the whole length of the olive, though in most sections, these two parts are connected. The medial one is by far the most important, especially over the frontal half of the olivary complex.

It principally enlarges dorsally and ventrally, as is demonstrated by a dorsal cap, and a distinct ventral knob (see Table 8, fig. 34).

In most frontal sections, however, this thickening has disappeared,

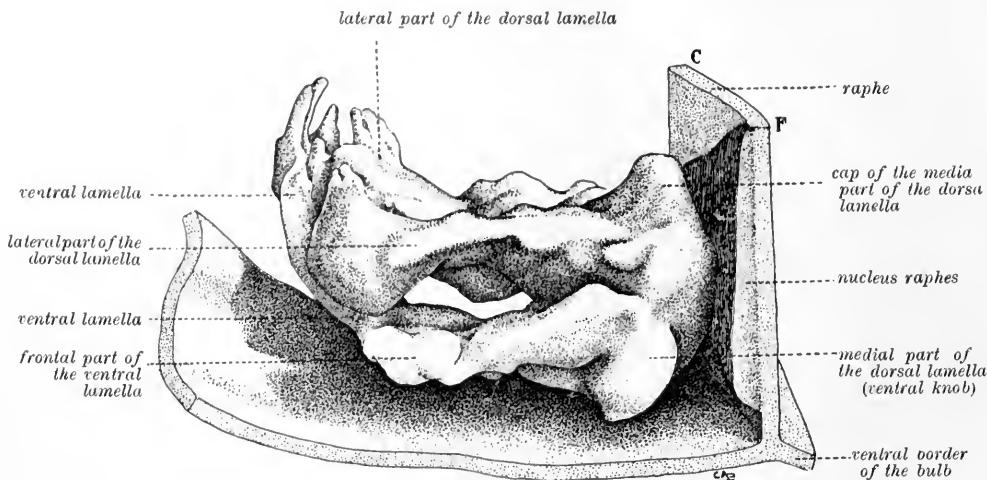


Fig. 34.

Inferior olive of *Spheniscus demersus* (L.) — $\pm 22 \times$ (frontal view).

while there are only cells left in the plane of the ventral lamella (Table 8, s. 36).

The *ventral lamella* reaches nearly as far caudally as the dorsal one.

Having on that caudal level a quite lateral position, it shifts medially in the following sections, being connected with the lateral part of the dorsal lamella (Table 8, s. 9).

A connection with the medial lamella in frontal regions, could nowhere be ascertained.

Speaking generally, the ventral lamella is represented by a lateral cell-accumulation.

The *reticular raphe-nucleus* has the usual form; it is well-developed.

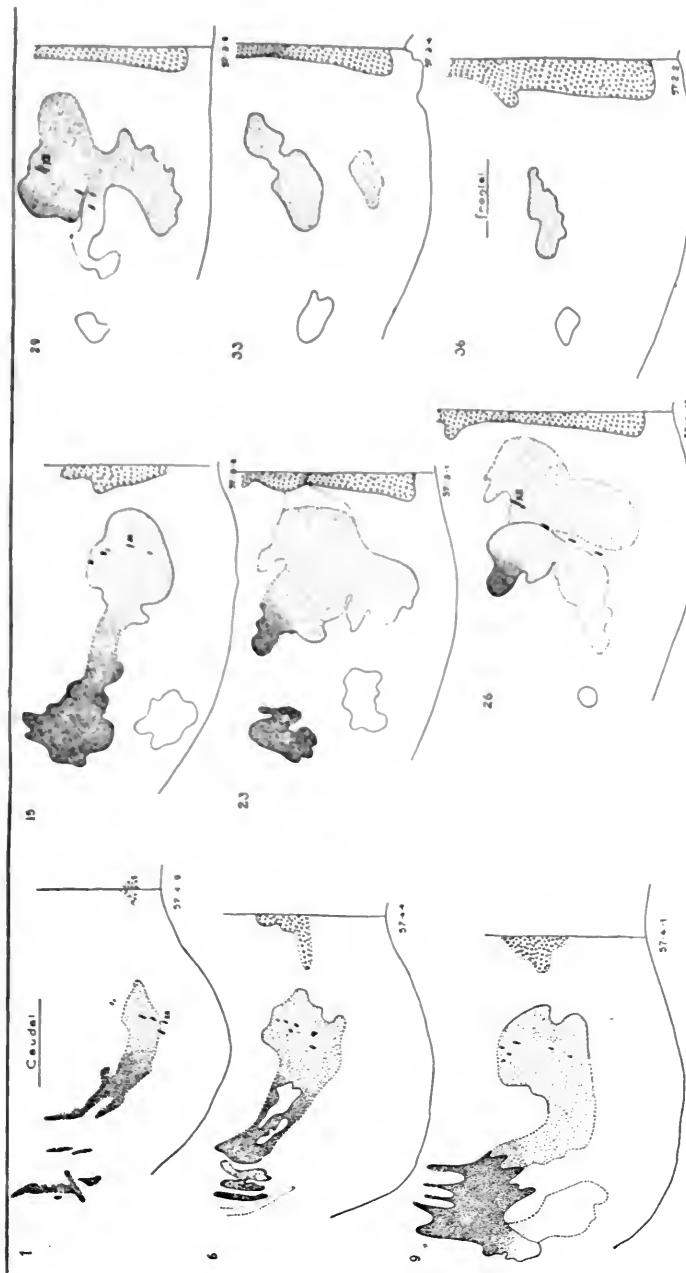


Table 8
Abbreviated order of sections through the inferior olive of *Spheniscus demersus* (L.).
Magnified 13.3 X.
Size of the section = 68 μ .

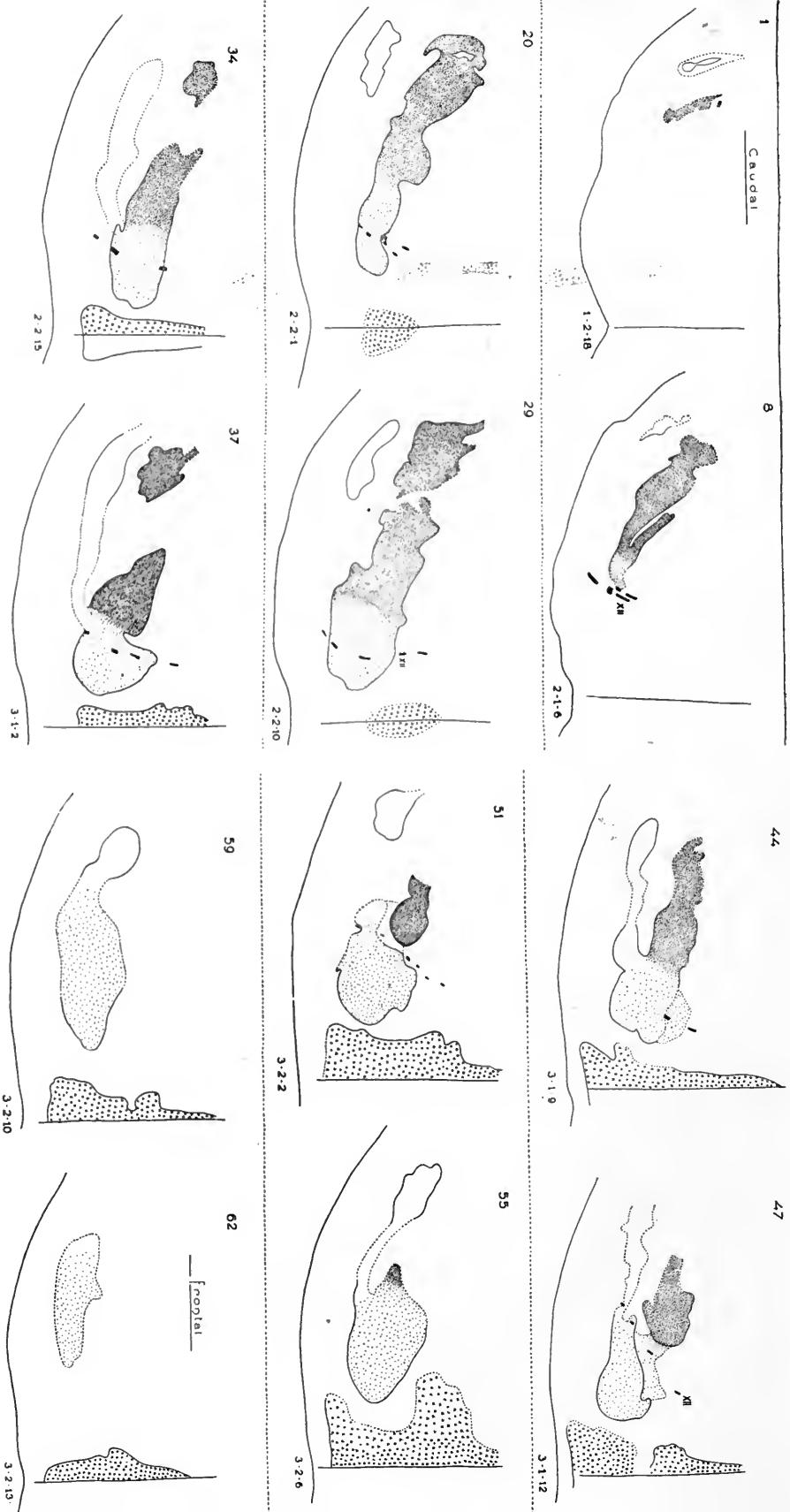


Table 9.
Abbreviated order of sections through the inferior olive of *Ciconia ciconia* (L.).

Size of the section = 60 μ .
Magnified 20 X.

Table 9b.
Abbreviated order of sections through the inferior olive of *Ciconia ciconia* (L.).

Magnified 20 X.

Ciconia ciconia (L.). — Waxreconstruction: fig. 35, Table 9.

Here the division of the *dorsal lamella* into a medial and a lateral part is possible throughout the entire length of the olive, the lateral part reaching rather far dorsally.

As is also the case with other birds, the caudal end of the olive lies in a plane, parallel to the raphe, while more frontally, it is parallel to the ventral border of the bulb (Table 9, s. 1). This is probably due

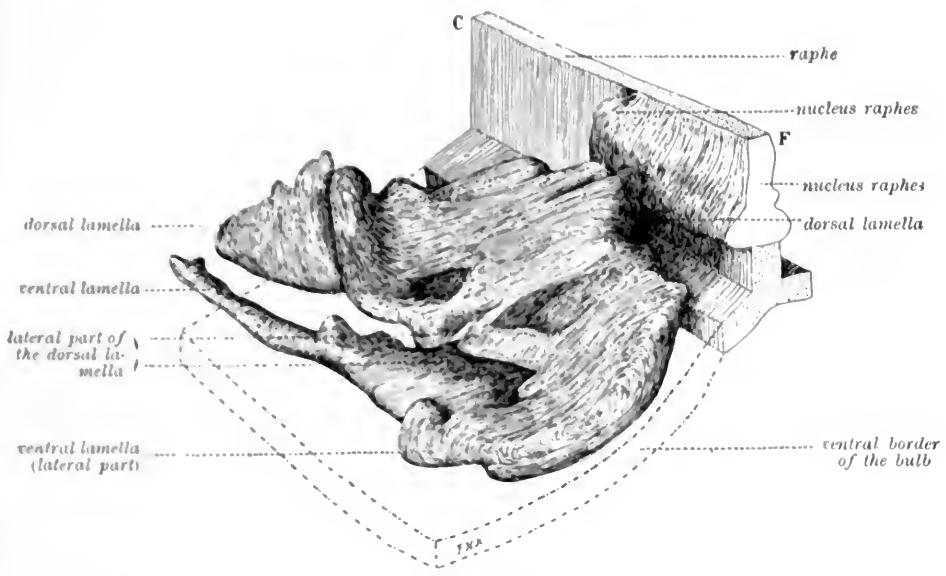


Fig. 35.

Inferior olive of *Ciconia ciconia* (L.) — 20 × (frontal and dorso-lateral view).

to the transition of the medulla spinalis into the oblongata, as is shown schematically in fig. 36.

The medial part turns and takes a ventral position, so that the most frontal olive-cells lie at the place of the former ventral lamella.

The *ventral lamella* remains chiefly lateral; its connection with the medial part is not distinct (see Table 9, s. 34, 37, 44 and 55), as is so often the case in Birds (vide supra).

The *reticular nucleus* is well-developed (Table 9, s. 51, 55).

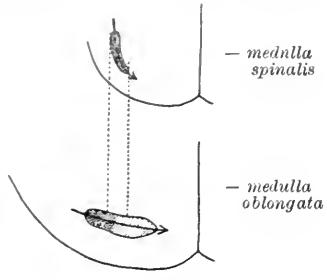


Fig. 36.
Scheme, showing the position of the olive with regard to the border of the bulb.

Cygnus olor Gm. — Waxreconstruction: fig. 37, Table 10.

The dorsal lamella is more or less distinctly divided into a medial and a lateral part throughout the entire length of the olive.

The medial part has a small dorsal cap and turns on a more frontal level, then lying in the same plane as the ventral lamella. The lateral part is connected with the ventral lamella on a caudal level, from which it is free more frontally.

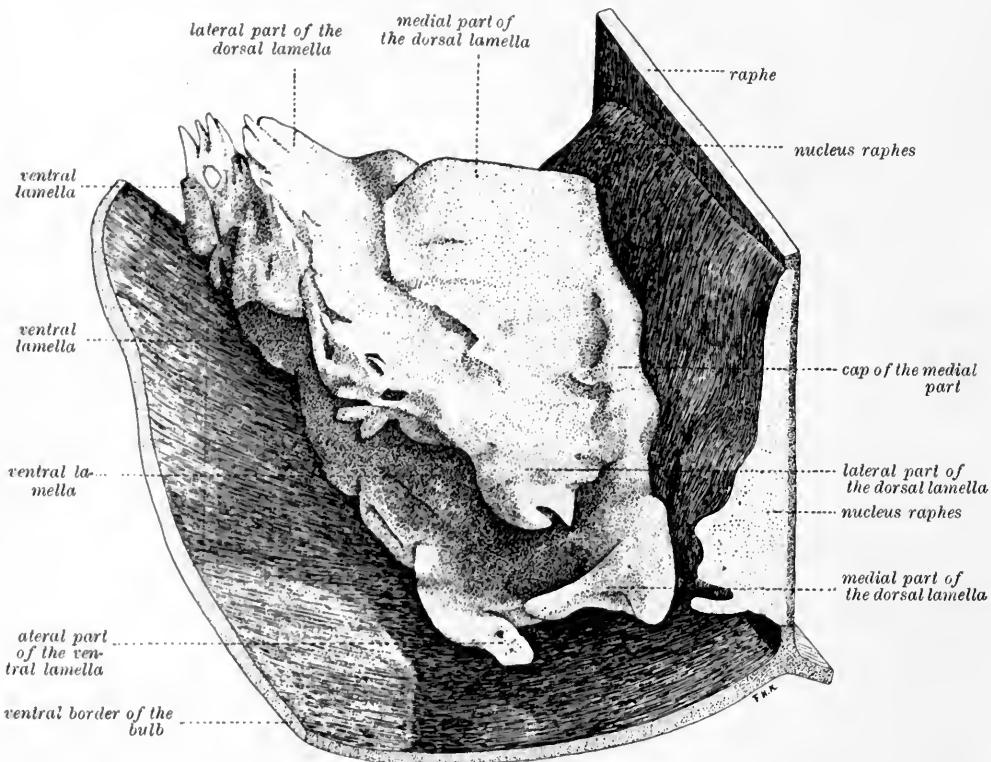


Fig. 37.

Inferior olive of *Cygnus olor Gm.* — 20 X (frontal and dorso-lateral view).

Finally it forms a lateral projection of the medial part.

The ventral lamella reaches as far caudally as the dorsal one; it is connected with the lateral part of the dorsal lamella on that level.

More frontally, it shifts medially, becoming situated ventrally of the dorsal lamella, whereas its position was quite lateral on a caudal level.

It then becomes connected with the medial part of the dorsal lamella; in its lateral part, however, the cells remain accumulated, while its medial connecting part is always indistinct.

Table 10bis.
Abbreviated order of sections through the olive of *Cygnus olor* Gm.

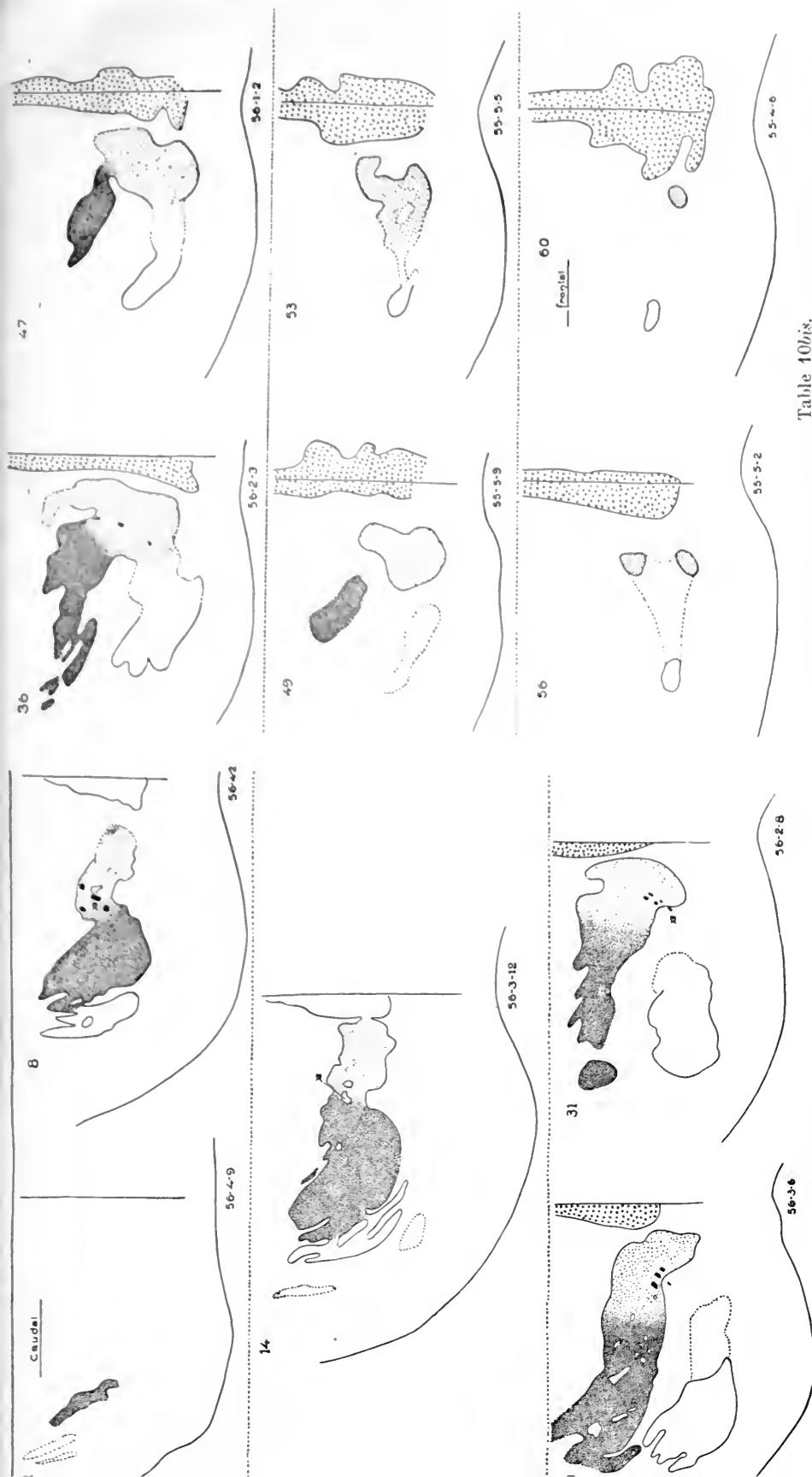


Table 10.
Abbreviated order of sections through the inferior olive of *Cygnus olor* Gm.
Size of the section = 60 μ .
Magnified 20 \times .

Most frontally, only this lateral part of the ventral lamella, remains, together with the medial part of the dorsal one.

The *reticular nucleus* is well-developed; it is still present in its full size, when the olive disappears frontally, having a long dorso-ventral dimension and a large ventral base.

Cathartes urubu (Vieill). — Waxreconstruction: fig. 38, Table 11.

In caudal sections, a division of the *dorsal lamella* into a medial and a lateral part can more or less be made. This lamella does not reach far laterally or dorsally. The cap is only poorly developed, but the ventral turning of the medial part is very striking.

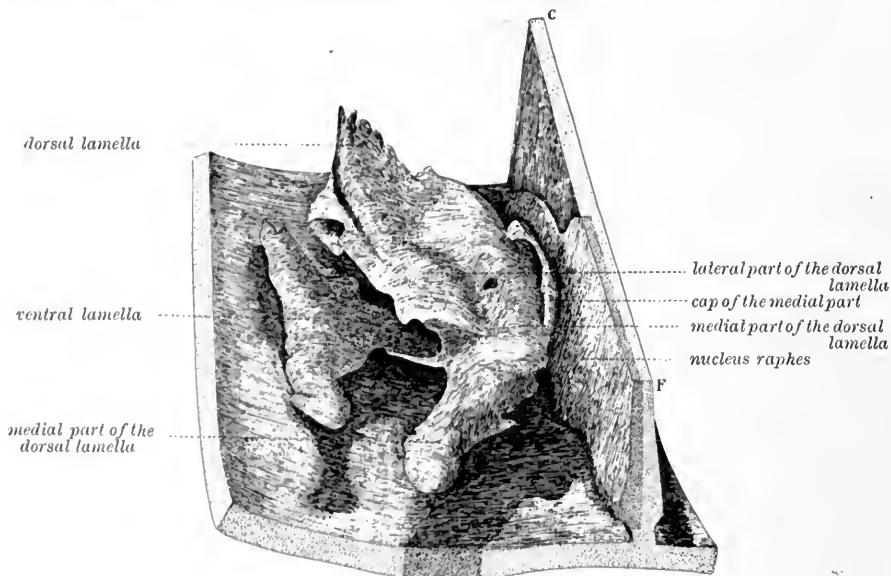


Fig. 38.

Inferior olive of *Cathartes urubu* (Vieill) — ± 20 × (frontal and dorsal view).

The *ventral lamella* is short and keeps a rather lateral position; its medial connection with the dorsal lamella is indistinct.

The *reticular nucleus* shows nothing particular (see fig. 38).

Haliaetus melanoleuca. — Waxreconstruction: fig. 39, Table 12.

Over a long distance, the *dorsal lamella* is an equally thick plate; only in a few sections, it can be divided into a lateral and a medial part (Table 12, s. 29—36); on a frontal level, only the latter, which is almost round, is present.

Of the *ventral lamella*, only the lateral part is distinct, a connection with the dorsal lamella is occasionally visible (Table 12, s. 29, 34).

The ventral lamella reaches as far frontally as the dorsal one, but much less caudally than is usual in Birds.

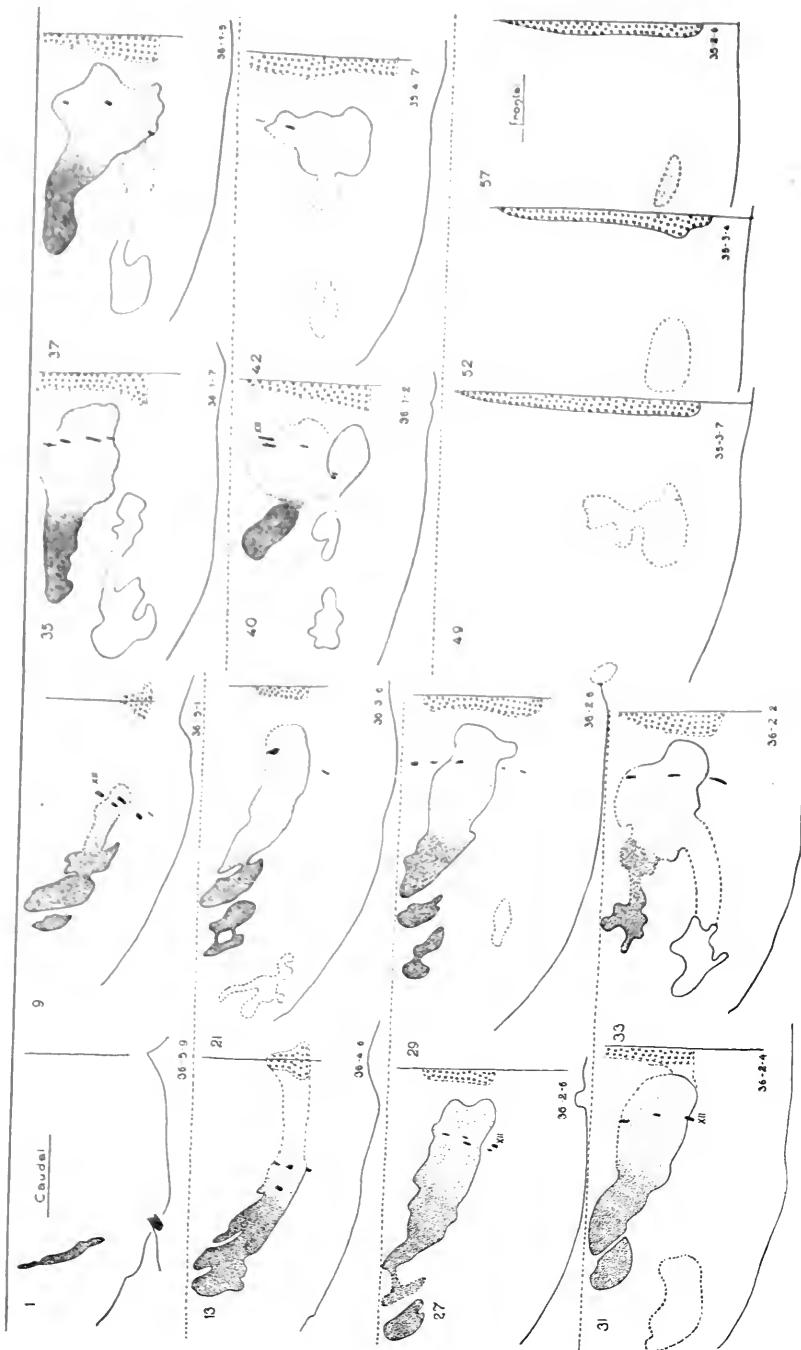


Table 14.

Abbreviated order of sections through the inferior olive of *Cathartes aura* (Vigili).
Magnified 43:3 \times .
Size of the section = 60 μ .

The thin reticular nucleus shows nothing particular.

Gallus gallus (L.) (domesticus). — Waxreconstruction: fig. 40, Table 13.

The olive is short and compact, and lies exactly at the transition of spinal cord into oblongata.

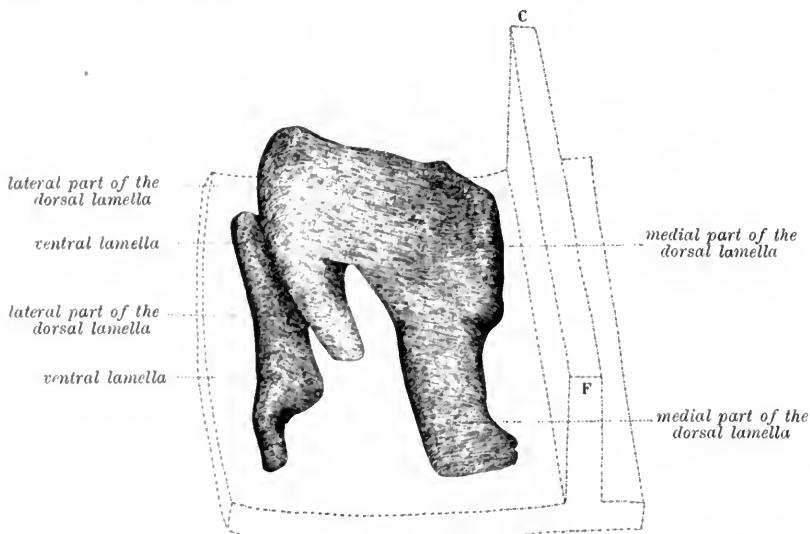


Fig. 39.

Inferior olive of *Haliaeetus melanoleuca* — 12.8 × (fronto-dorsal view)

On the level of this transition, the oblongata bulges rather abruptly ventralward; in the thus formed protrusion the olive is found (Chiefly its ventral lamella, Table 13, s. 8).

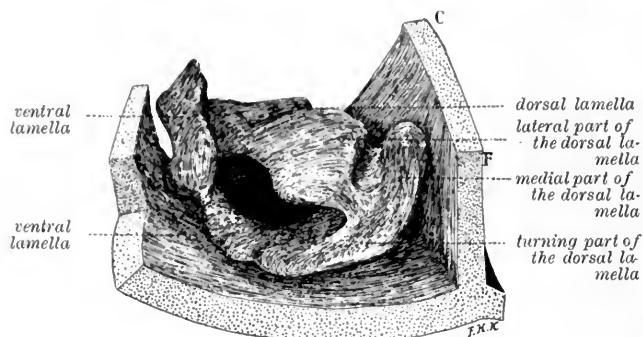


Fig. 40.

Inferior olive of *Gallus gallus (L.) domesticus* — 20 × (fronto-dorsal view).

tral lamella, shows a particular form in Gallus.

In very caudal sections, the *dorsal lamella* lies quite near the border of the bulb. When the bulb enlarges ventrally, it gets a more dorsal

In consequence of this, the olive, especially the ven-

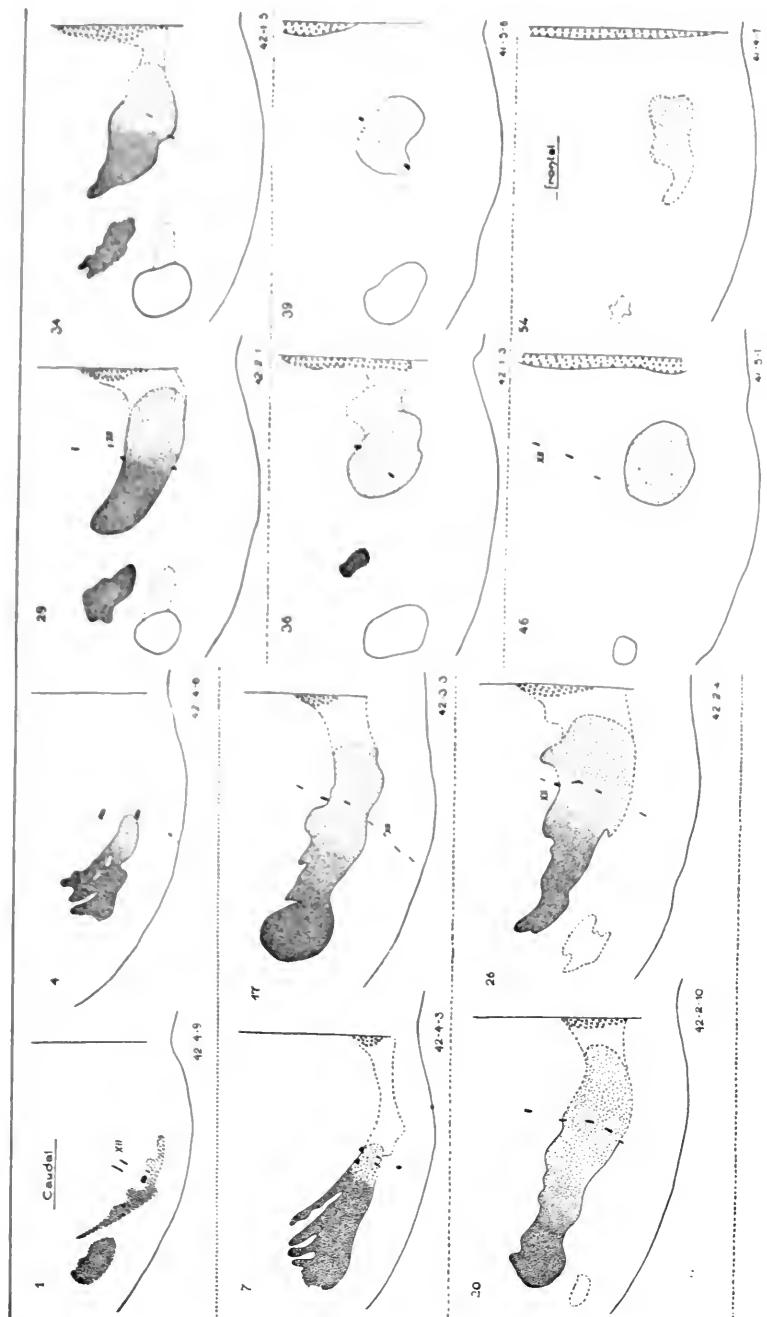


Table 12.
 Abbreviated order of sections through the inferior olive of *Haliaetus melanoleucus*.
 Size of the section = 60 μ .
 Magnified 13.3 \times .

position, it is here divided into a medial and a lateral part, connected by a more indistinct strand of cells. The medial part has the usual cap and is most frontally situated in a plane parallel to the raphe; the lateral part is placed perpendicularly on the medial one (Table 13, s. 18, 21).

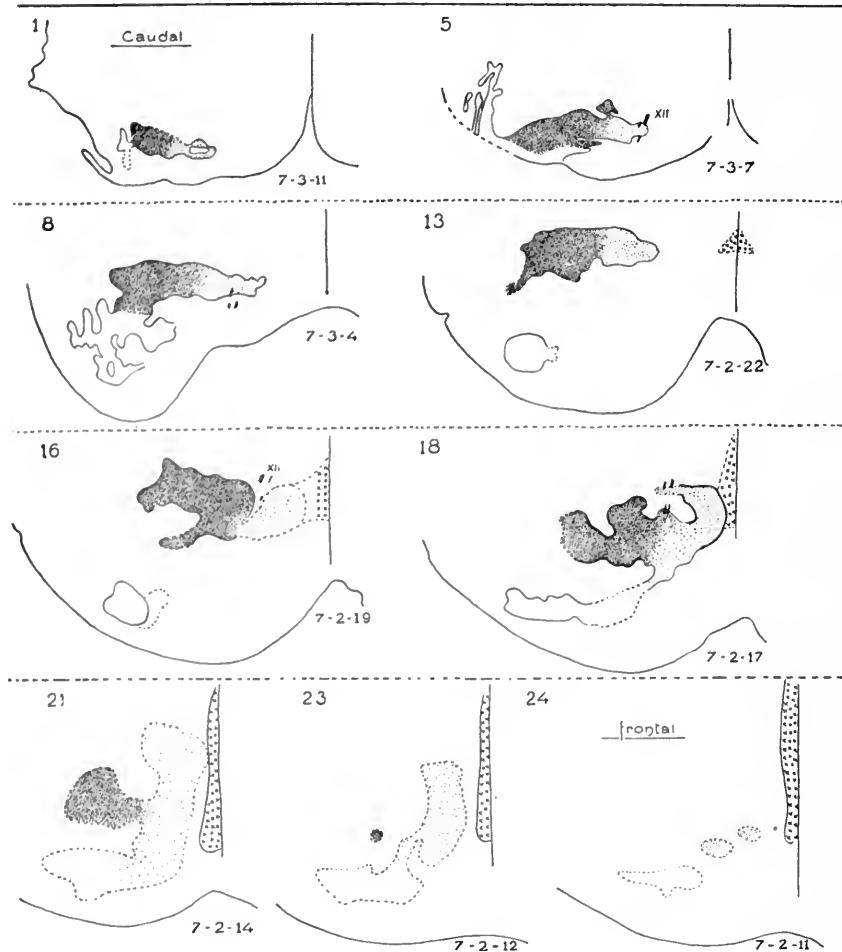


Table 13.

Abbreviated order of sections through the inferior olive of *Gallus gallus* (L.)

Size of the section = 50 μ .

Magnified 20 X.

The *ventral lamella* reaches nearly as far caudally as the dorsal one, lying on that level quite laterally of the latter (Table 13, s. 5).

More frontally, it sinks, as it were, into the ventral protrusion of the bulb; still more frontally, it is connected with the dorsal lamella.

Its lateral part is distinct and round; the connecting strand is again indistinct; it reaches, however, most frontally.

The *reticular nucleus* shows nothing remarkable.

Lophortyx californicus (Shaw & Nodd). — Waxreconstruction: fig. 41, Table 14.

This olive so much represents the typical olive-model of Birds in general, that I shall defer its description until I give the general points and the peculiarities of frequent occurrence, of the avian olive.

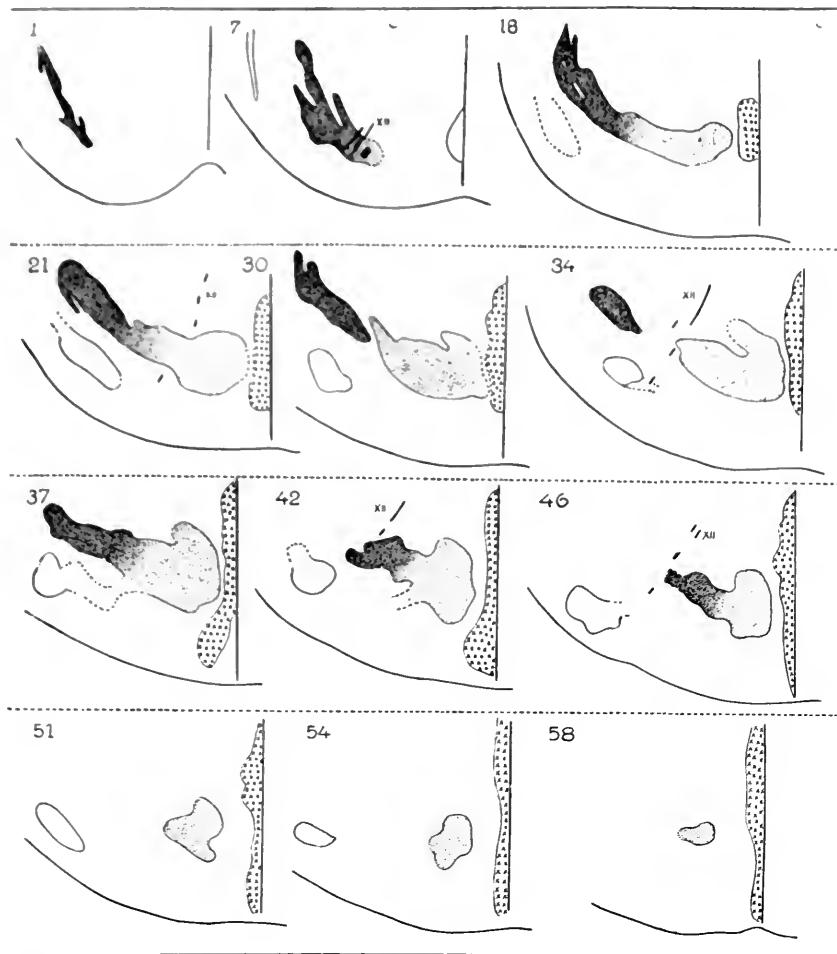


Table 15.

Abbreviated order of sections through the inferior olive of
Grus japonensis (P. L. S. Müller).

Size of the section = 60 μ .

Magnified 20 \times .

Grus japonensis (P. L. S. Müller). — Table 15.

In caudal regions, the *dorsal lamella* is undivided. More frontally, a lateral and a medial part can be distinguished, which are once more united into one lamella on a still higher level.

The lateral part then forms a small projection of the larger medial part, which has become an almost round nucleus near the raphe, showing a dorsal cap.

Whereas, speaking generally, the dorsal lamella is parallel to the ventral border of the bulb, its medial part is parallel to the raphe in a frontal region.

It is the most frontal part of the olfactory complex.

The *ventral lamella* in *Grus* reaches far caudally; on that caudal level, it has a quite lateral position (Table 15, s. 7); more frontally, it shifts medially, so that it becomes situated ventrally of the dorsal lamella, with which it is connected only by a bridge of a few cells.

This connecting part of the ventral lamella remains very indistinct and has even disappeared in higher sections.

Speaking generally, one can say that the ventral lamella is only represented by a lateral cell-accumulation.

The *reticular nucleus* (nucleus raphe or nucleus reticularis inferior) has the usual shape.

It appears caudally when the olive approaches the raphe; in the following sections, both nuclei are so near each other, that they can hardly be separated in Weigert-preparations. More frontally, the medial part of the olfactory complex diverges from the raphe, while at the same time the nucleus reticularis increases, especially its dorso-ventral dimension.

When the olive ends frontally, the nucleus raphe is still present in its full size.

Larus argentatus. (Gm). — Table 16.

The *dorsal lamella* is undivided over the caudal half of the olive, (Table 16, s. 1—16).

More frontally, (Table 16, s. 16, a. s. o.) a medial and a lateral part can be distinguished. The medial part turns, becomes parallel to the raphe, and, still more frontally, parallel to the ventral border of the bulb, at the same time diverging from the raphe (Table 16, s. 22—44); it is the most frontal olive-part.

The *ventral lamella*, much less developed than the medial one, reaches as far caudally as the latter. More frontally, it is connected with the dorsal lamella, thus forming a lateral hilus.

The connecting part of the ventral lamella is indistinct in most

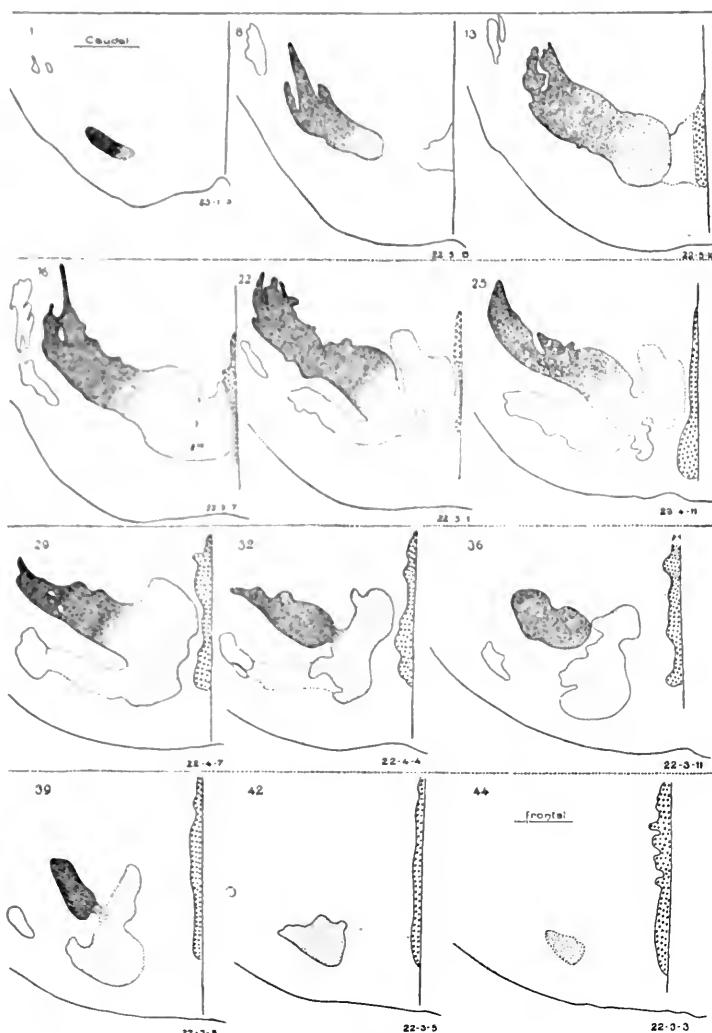


Table 16.
Abbreviated order of sections through the inferior olive of
Larus argentatus (Gm.).

Size of the section = 60 μ .

Magnified 13.3 \times .

sections; its lateral part, which is always distinctly visible, reaches most frontally (Table 16, s. 36—42).

The *reticular nucleus* shows nothing particular.

Columba guinea L. — Waxreconstruction: fig. 42, Table 17.

Columba livia Bonn. (*domestica neonata*). — Table 18.

Both were difficult to draw and to reconstruct.

I only modelled the olive of *Columba guinea*. In this bird, only the *dorsal lamella* is distinct; it shows the common long-stretched type in

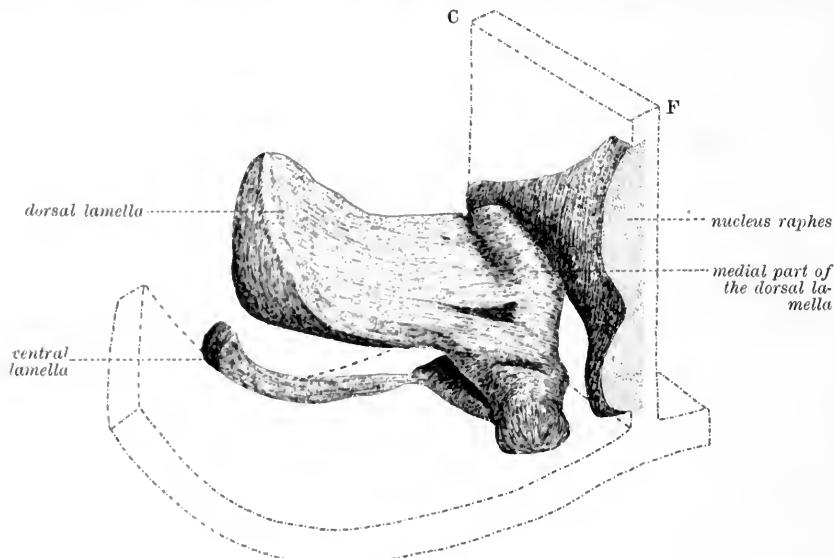


Fig. 42.
Inferior olive of *Columba guinea L.* — 30 ×
(frontal and dorso-lateral view).

its caudal half; more frontally, the medial accumulation, with an indication of the cap and the turning ventrally, can be seen.

The *ventral lamella* is so indistinct, that it can hardly be reconstructed. Only the part in connection with the dorsal lamella seems to be present and more laterally also a small accumulation is visible in a few sections (Table 17, s. 12).

Columba livia Bonn. also shows over a great distance the longstretched type of the *dorsal lamella*; a small medial thickening is to be seen.

Also the *ventral lamella* is distinctly present; most cells are accumulated in its lateral part, but also the connection with the dorsal lamella is distinct.

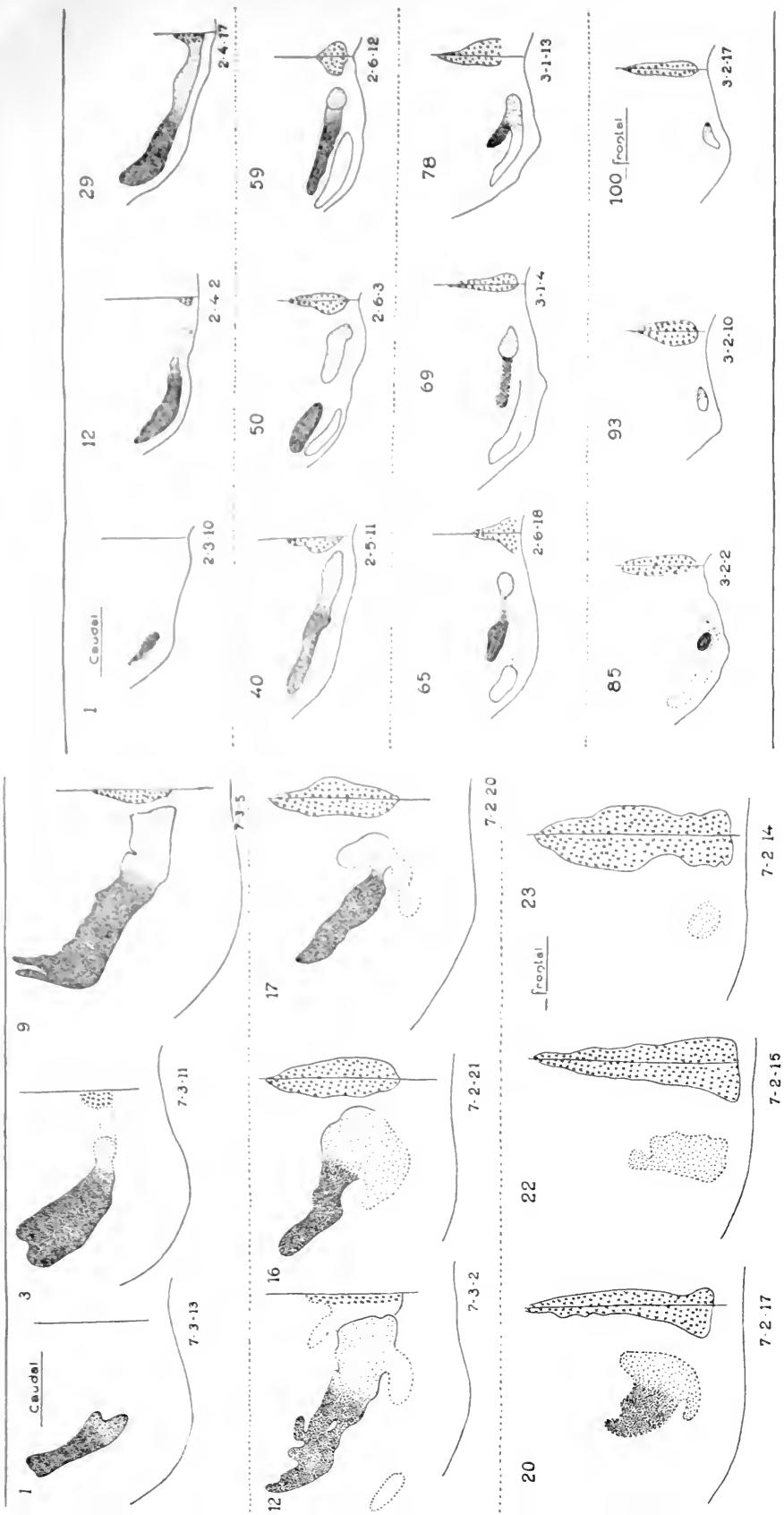
The *reticular nucleus* in both Columbae is well developed; like in all birds, it is still present in its full size, when the olive disappears frontally.

Size of the section = ?
Magnified 20 X.

Table 17.
Abbreviated order of sections through the inferior olive of *Columba guineae* L.
Size of the section = 50 μ .
Magnified 20 X.

Size of the section = ?
Magnified 26 X.

Table 18.
Abbreviated order of sections through the inferior olive of
Columba livia Bonn.



Cacatua roseicapilla Vieill. — Waxreconstruction: fig. 43 and 44, Table 19.

What strikes one most in the olive of *Cacatua* is the huge development of the medial part of the *dorsal lamella*.

The lateral part is much less developed, only worth mentioning in

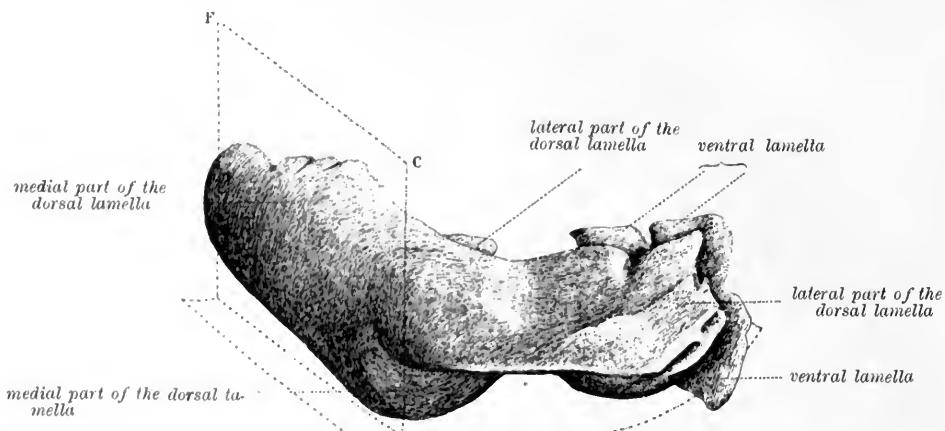


Fig. 43.

Inferior olive of *Cacatua roseicapilla* Vieill. $27 \times$ (caudal and medial view).

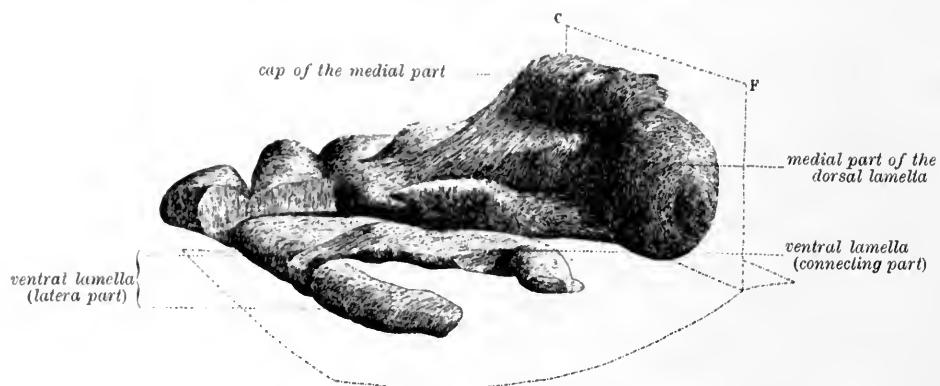


Fig. 44.

Inferior olive of *Cacatua roseicapilla* Vieill. — $30 \times$ (frontal and lateral view).

caudal sections and in frontal sections as a small lateral projection of the medial part (Table 19, s. 35, 41, 43).

The medial part is large in all dimensions (as can be seen in the wax-reconstruction and in Table 19) and more frontally it has a cap.

The *ventral lamella* is well-developed, it reaches nearly as far caudally as the dorsal one. In the above-mentioned caudal sections it is over a

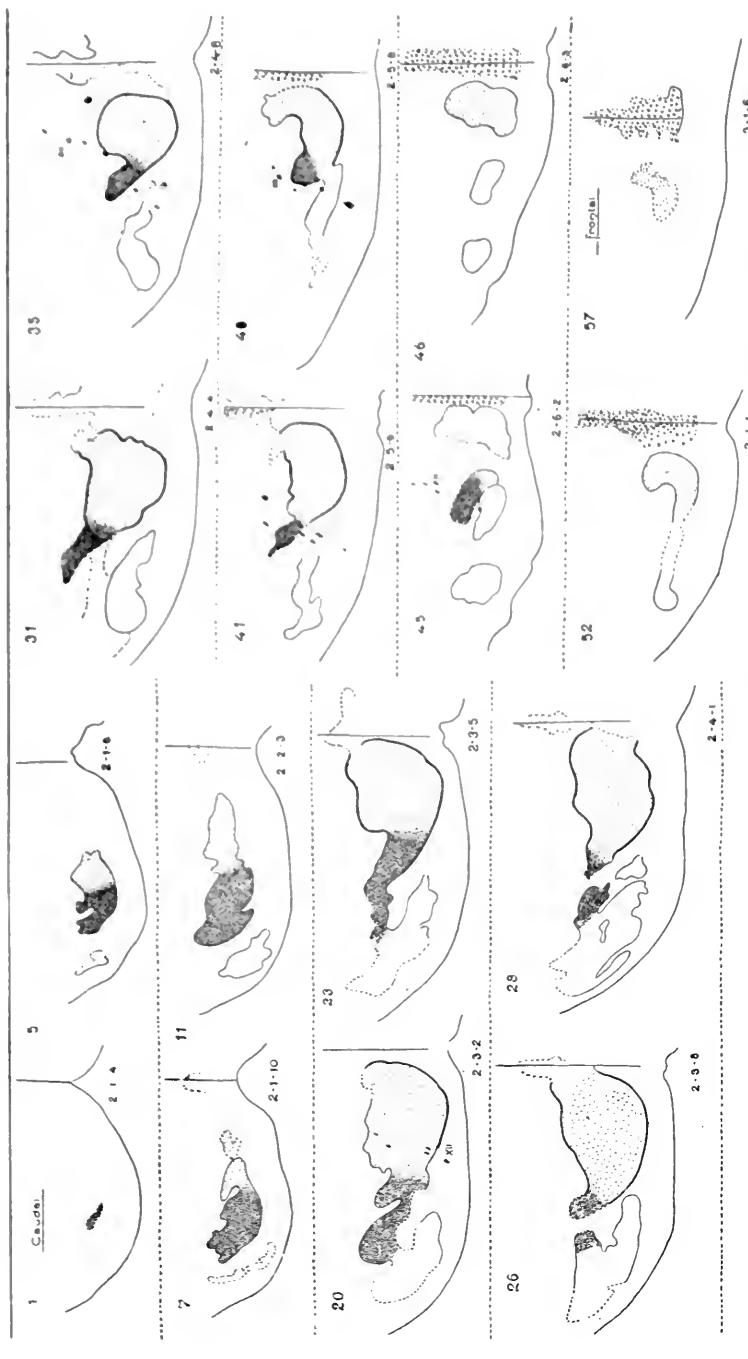


Fig. 49.
Abbreviated order of sections through the inferior olive of *Cacatua roseicapilla* Vieill.
Size of the section = 46 μ .
Magnified 13.3 \times .

short distance connected with the lateral part of the dorsal lamella; more frontally it is free from this part, but connected with the medial one.

On a frontal level the ventral lamella is interrupted; only the most lateral part and a more medial one are dis-

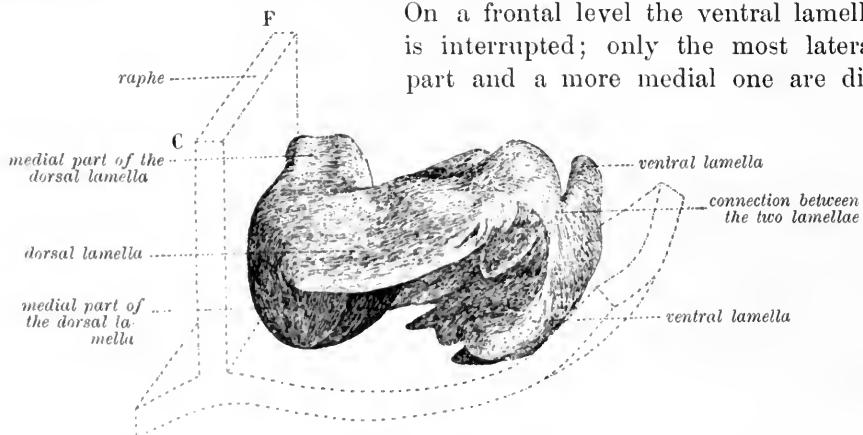


Fig. 45.
Inferior olive of *Palaeornis eupatria* (L.) — 25 X (caudal view).

tinctly visible. (Table 19, s. 45, 46); yet they belong to one lamella (Table 19, s. 52).

The reticular nucleus is as usual.

Palaeornis eupatria (L.). — Waxreconstruction: figs. 45 and 46, Table 20.

This olive, otherwise difficult to inter-

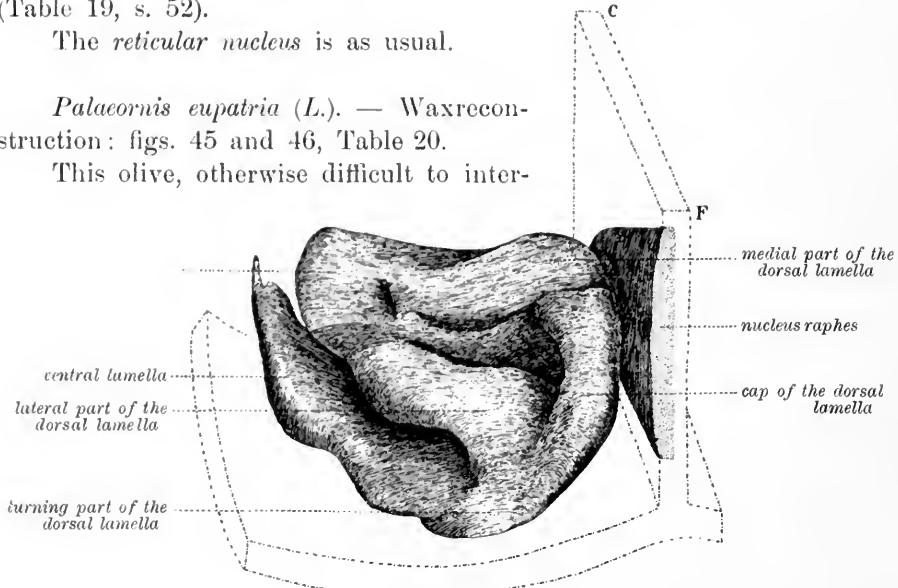


Fig. 46.
Inferior olive of *Palaeornis eupatria* (L.) — 25 X (frontal and dorsal view)

prete, is easily understood with the knowledge of the olive of the other prete, is easily understood with the knowledge of the olive of the other birds and especially of Cacatua.

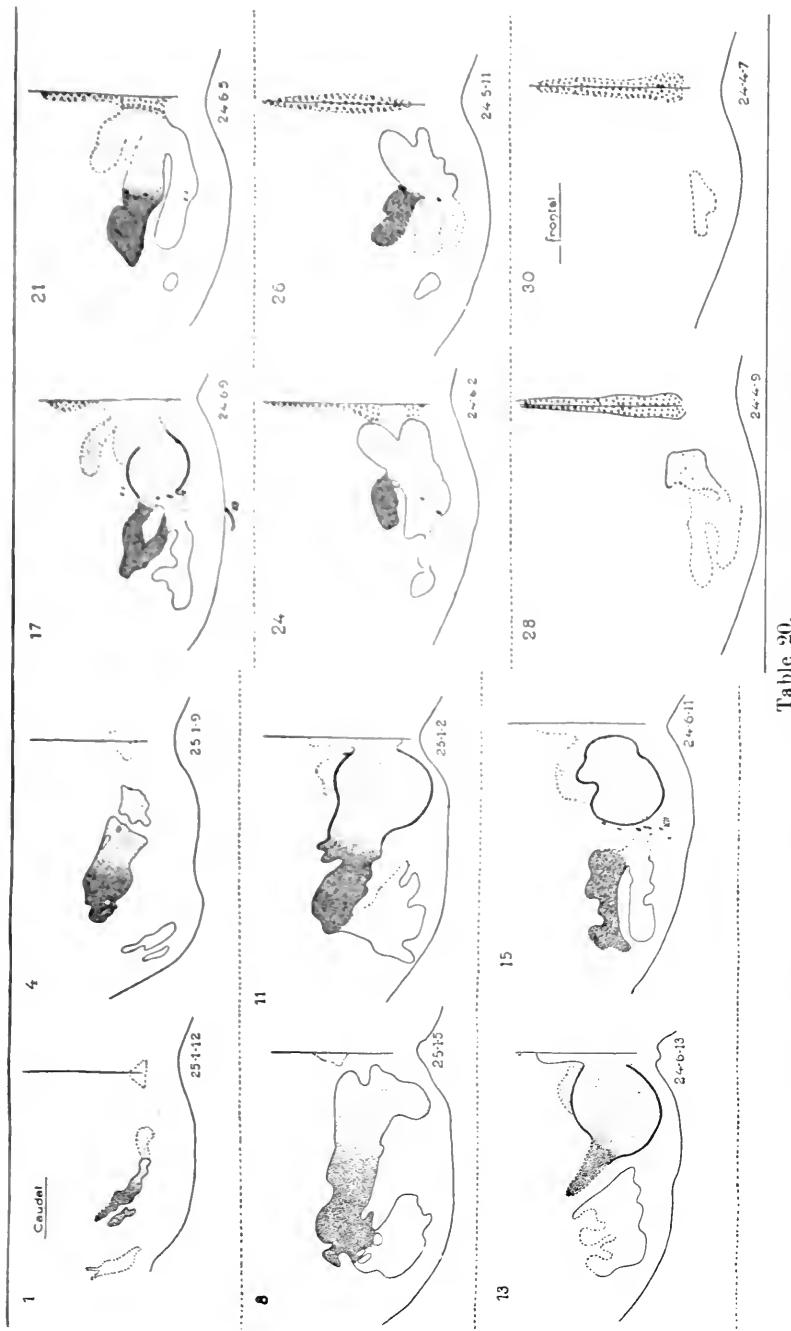


Table 20.
Abbreviated order of sections through the inferior olive of *Palaeomys eupatricia*.
Size of the section = 60 μ .
Magnified 13.3 \times .

The *dorsal lamella* has also in this bird a strongly developed medial part; the lateral part, caudally united with the medial one, is a little higher separated from it and connected with the ventral lamella. More frontally it is only a rather small lateral projection of the medial part.

The *ventral lamella*, also well developed here, reaches far caudally, is more frontally connected with the lateral part of the dorsal lamella, still more frontally free from it and connected with the medial part of the dorsal lamella.

The lateral part of the ventral lamella is the most distinct.

The *reticular nucleus* is very poorly developed.

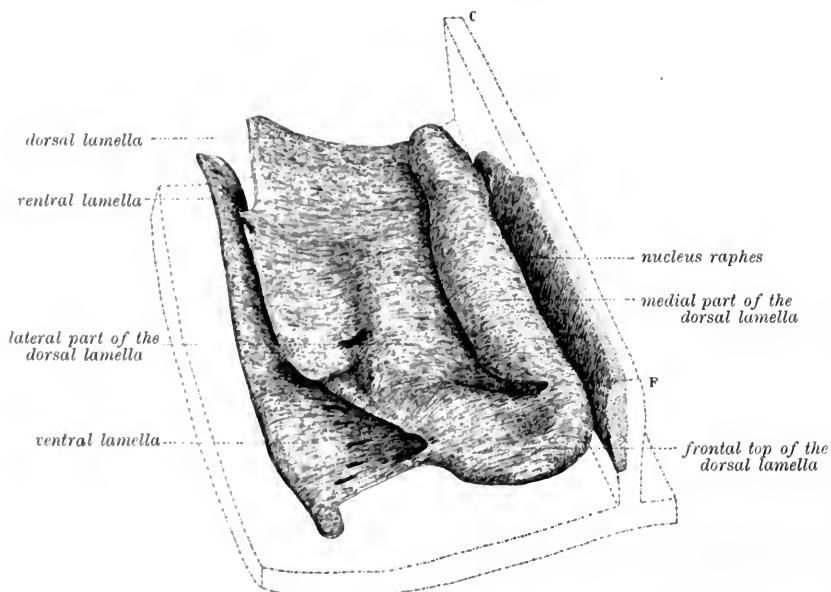


Fig. 47.

Inferior olive of *Ara psittacus* — 22.5 X (frontal and dorso-lateral view).

Ara psittacus. — Waxreconstruction: figs. 47 and 48, Table 21.

Like in all Parrots, the most striking feature in Ara is the enormous development of the medial part of its *dorsal lamella* (fig. 48).

Also here, both lamellae reach unto the same caudal level, the lateral part of the dorsal lamella is connected with the ventral lamella in a few sections; more frontally, the lamellae are free from each other, and still more frontally, the ventral lamella is in the usual way connected with the dorsal one, thus forming a lateral hilus.

The medial part of the dorsal lamella is strikingly developed, as has been mentioned above; more frontally, it turns 180° and finally lies

in the same plane as the ventral lamella. In these frontal regions, the lateral part, which only in a few sections is free from the medial one (Table 21, s. 62), forms a small projection of the latter.

The lateral part of the *ventral lamella* is best developed and distinctly visible; the medial connecting part is less distinct and often interrupted (fig. 47). Most frontally, cells are only present in a plane parallel with the border of the bulb and probably belonging to the inverted medial part of the dorsal lamella.

The *reticular nucleus* is poorly developed (and for that reason, not drawn).

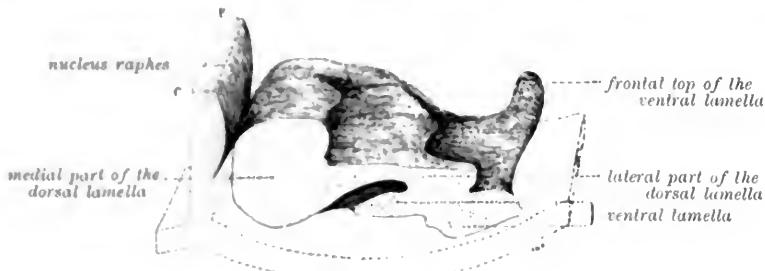


Fig. 48.

Frontal part of the inferior olive of *Ara psittacus* — 22.5 × (caudal view).

Athene nocturna (Scop.). — Table 22.

The olive in *Athene* is rather short.

Its dorsal lamella is for the greater part undivided; only on a frontal level, a division can be made into a rounder medial part and a lateral one perpendicular on it (Table 22, s. 21, 23). In most frontal sections, the medial part turns in the usual way about 180°, reaching rather far ventrally (Table 22, s. 26—28).

The *ventral lamella* reaches less far caudally than the dorsal one. Being situated rather far laterally in its most caudal sections, it extends on higher levels more and more medially and becomes connected with the dorsal lamella. Thus a hilus is formed, which opens laterally.

The lateral part of the ventral lamella is the most distinct, as I have already described with so many birds. The most frontal olive-part corresponds to the point of connection between the two lamellae more below.

The *reticular nucleus* has the usual form; in our caudo-frontal examination of the series, we see it gradually increase, chiefly in its dorso-ventral dimension.

In most frontal sections through the olive, it is fully developed and shows a large base.

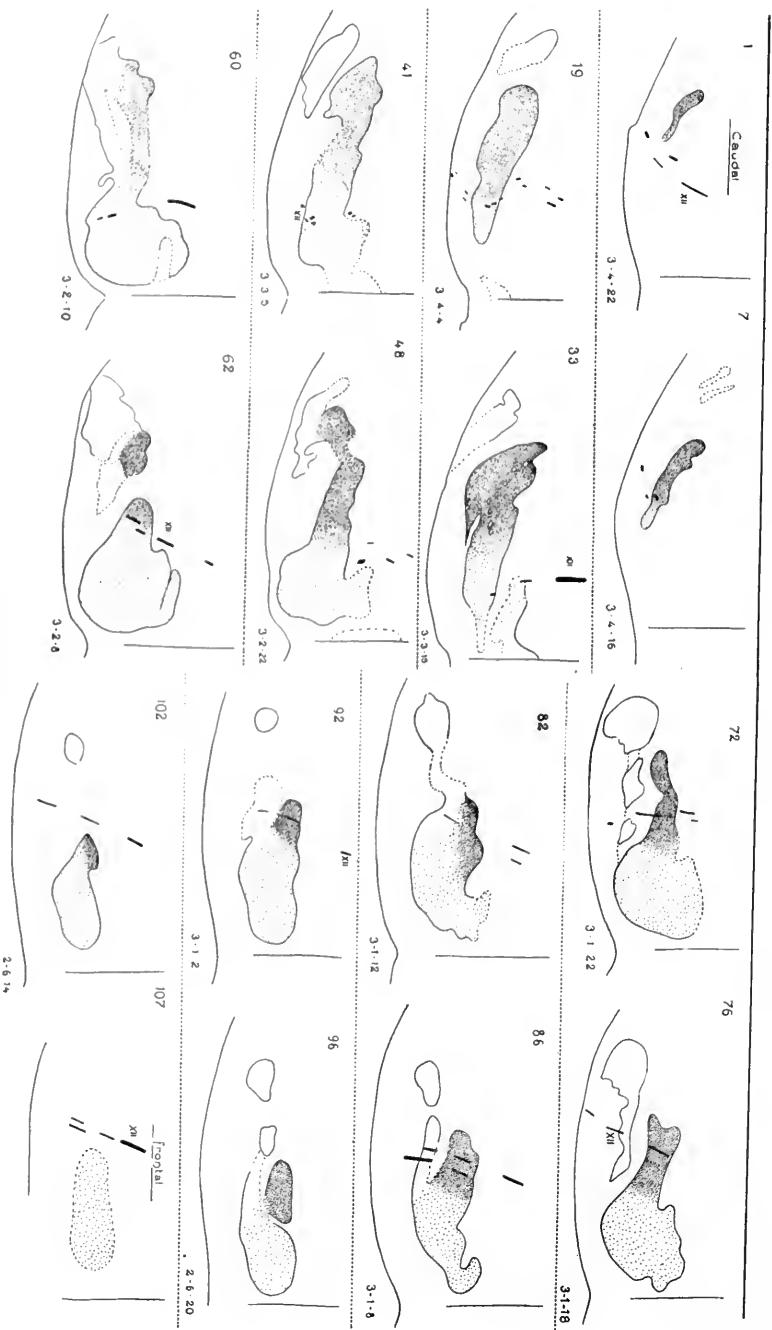


Table 21.

Abbreviated order of sections through the inferior olive of *Ara psittacula*.
Size of the section = 30 μ .
Magnified $\pm 13.3 \times$.

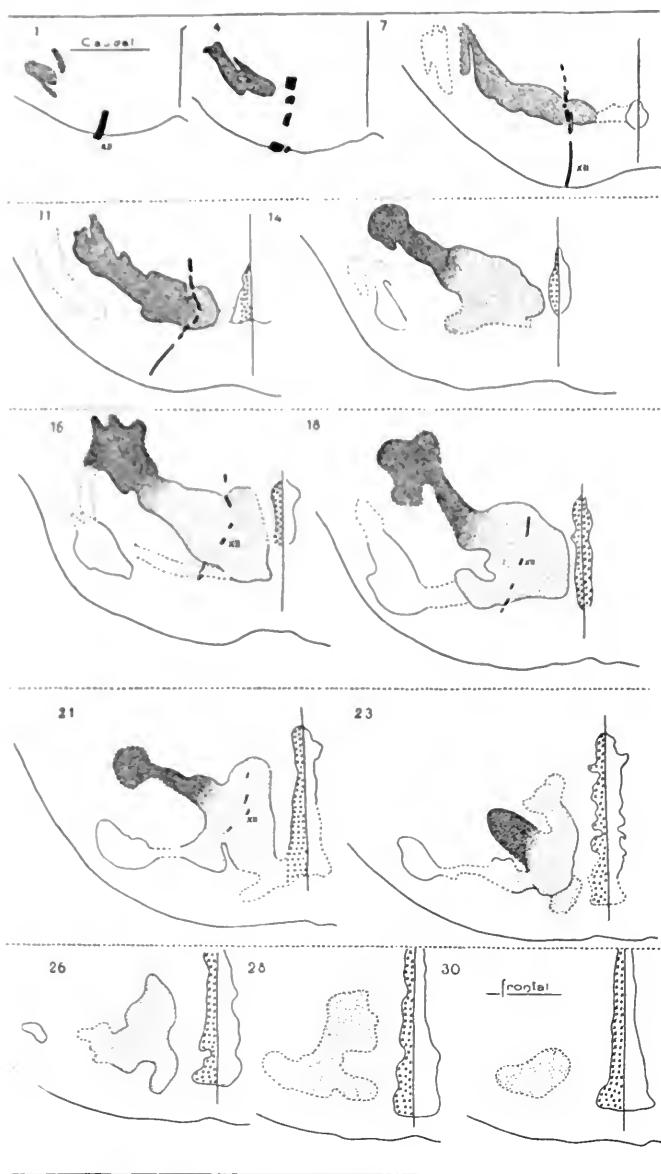


Table 22.
Abbreviated order of sections through the inferior olive of
Athene nocturna. (Scop.)

Size of the section = 60 μ . Magnified 13.3 \times

Sturnus vulgaris (L.). — Waxreconstruction: fig. 49, Table 23.

The medial and the lateral part of the *dorsal lamella* are nowhere separated in this bird. The medial part shows the common cell-accumulation near the raphe and has a dorsal cap; the lateral part, its most caudal part excepted, is difficult to distinguish from the ventral lamella.

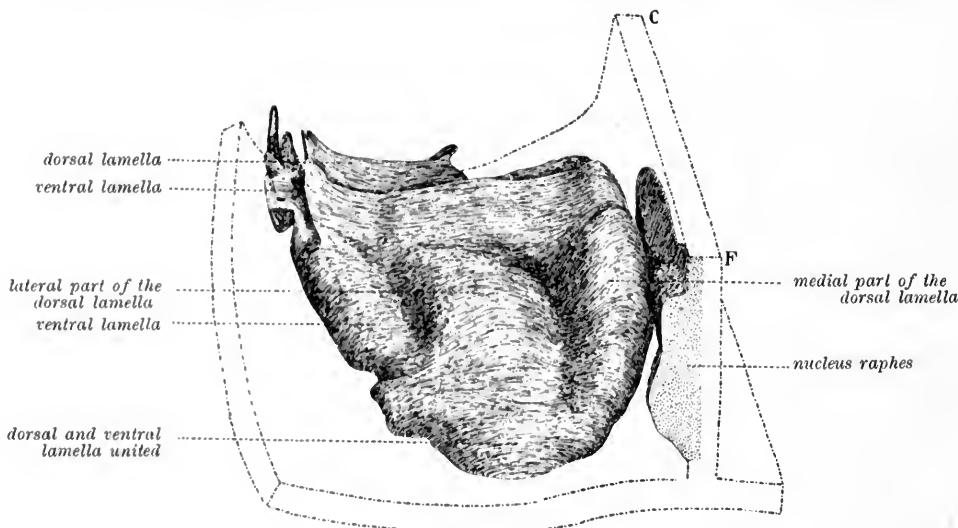


Fig. 49.

Inferior olive of *Sturnus vulgaris* L. — 30 X (frontal and dorsal view).

This *ventral lamella* reaches a little more caudally than the dorsal one; more frontally it is not to be separated from the lateral part of the dorsal lamella — the layer of fibres that usually separate the two lamellae being very thin and interrupted —; so in frontal regions, there seems to be only one lamella, though an indication of a lateral part of the dorsal lamella can be seen (Table 23, s. 25 and 29).

The *reticular raphe-nucleus* shows nothing particular.

Pratincola rubicola (L.). — Table 24.

At the transition of medulla spinalis into medulla oblongata, the bulb suddenly enlarges ventrally, as has already been described in *Gallus*.

The caudal end of the olive lies in the thus formed ventral protrusion (Table 24, s. 1—18). In consequence of this, the form of the caudal half of the olive is more compact than it usually is.

Over its frontal half, the *dorsal lamella* can be divided into a medial and a lateral part (Table 24, s. 18—26); the medial one is the most important; it reaches rather far dorsally and is placed parallel to the

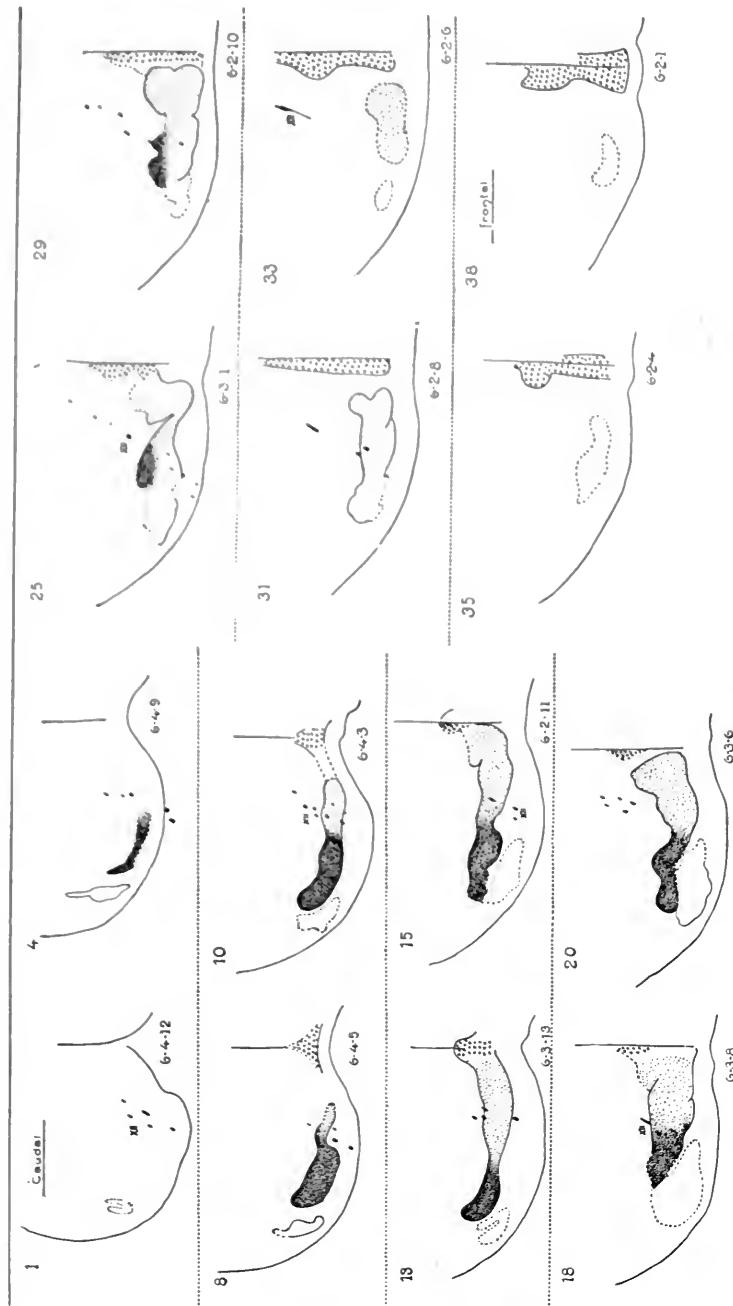


Table 23.
Abbreviated order of sections through the inferior olive of *Styrax vulgaris* L.
Size of the section = 50 μ . Magnified 13.3 \times

raphe. More frontally, the lateral part is only a small lateral outgrowth of the medial one (Table 24, s. 26).

The *ventral lamella* is in a few sections connected with the lateral part of the dorsal lamella (Table 24, s. 18—23); more frontally it is connected with the medial part. The complex: ventral lamella and medial part of the dorsal lamella reaches most frontally.

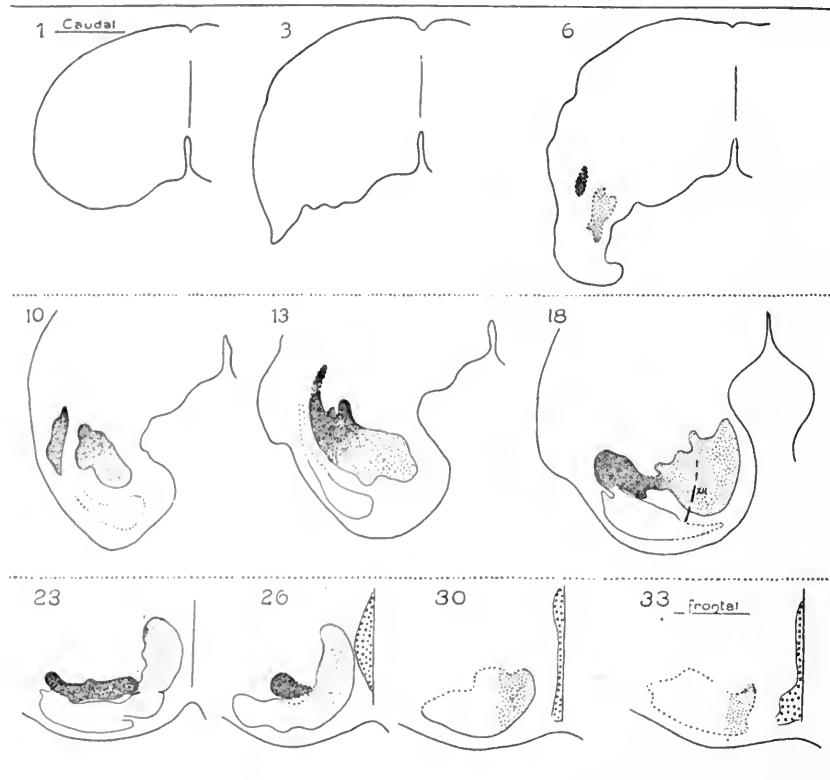


Table 24.

Abbreviated order of sections through the inferior olive of *Pratincola rubicola* (L.).
Size of the section = 25μ . Magnified 20 X.

The *reticular nucleus* appears caudally in the raphe on the level of the medial olive-part, approaching the diameter, like in other birds, though the olive in *Pratincola* reaches the raphe on a much more frontal level.

General morphology of the olive in Birds.

While describing *Lophortyx californicus* (Shaw & Nodd) — Waxre-

construction: fig. 41, Table 14, I can at the same time give the general morphology of the avian olive.

We find two lamellae, both parallel to the ventral or ventro-lateral border of the bulb, which in a frontal region, are connected at their medial ends, so that a hilus appears laterally.

Caudally, the *dorsal lamella* shows a flat form; more frontally its *medial part*, situated near the raphe broadens and shows a *dorsal cap*. The lateral part of the dorsal lamella is on this level also situated more medially, while it lies more or less *perpendicularly* on the *medial part*.

This latter has turned 90° and is now situated in a plane, parallel to the raphe.

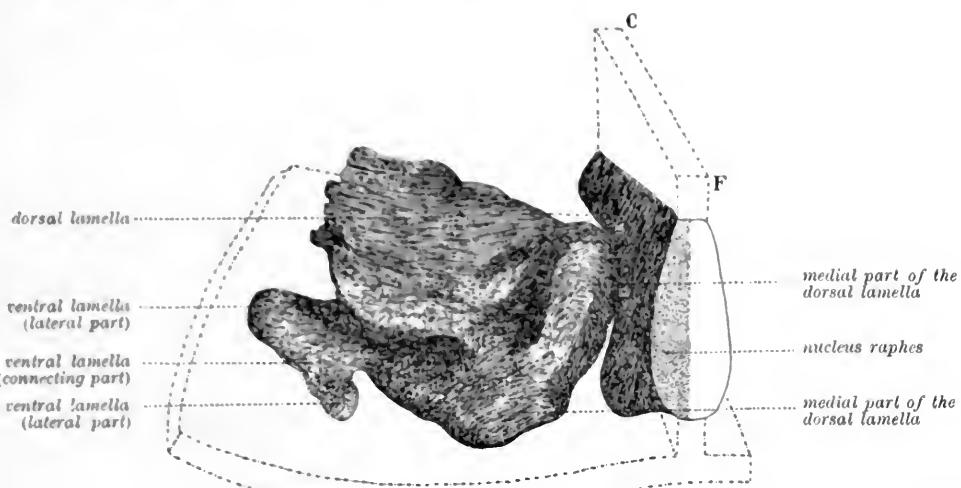


Fig. 41.
Inferior olive of *Lophortyx californicus* (Shaw & Nodd) — 30× (fronto-dorsal view).

The lateral part then ends and the *medial part*, bending still further, is again situated more parallel to the ventral border of the bulb in the plane of the ventral lamella, at the same time diverging from the raphe.

Of the ventral lamella, reaching less caudally than the dorsal one, the *lateral part* is developed best of all, its *medial part*, which connects the ventral lamella with the dorsal one, being thin and containing only a few scattered cells.

The *lateral part* of the ventral lamella reaches a little more frontally than this indistinct connecting one.

The *reticular nucleus* appears in the raphe on about the level of the

olive approaching it. If the olive reaches the diameter on a higher level, the nucleus reticularis too appears more frontally (*Pratincola*); in other words: the meeting-point of olive and raphe coincides with the caudal end of the reticular nucleus. It increases in a frontal direction and is generally separated from the olive by a strand of fine fibres, though both cellbodies touch each other, when the medial olive-part is largest.

When the olive ends frontally, the reticular nucleus is still present in its full size.

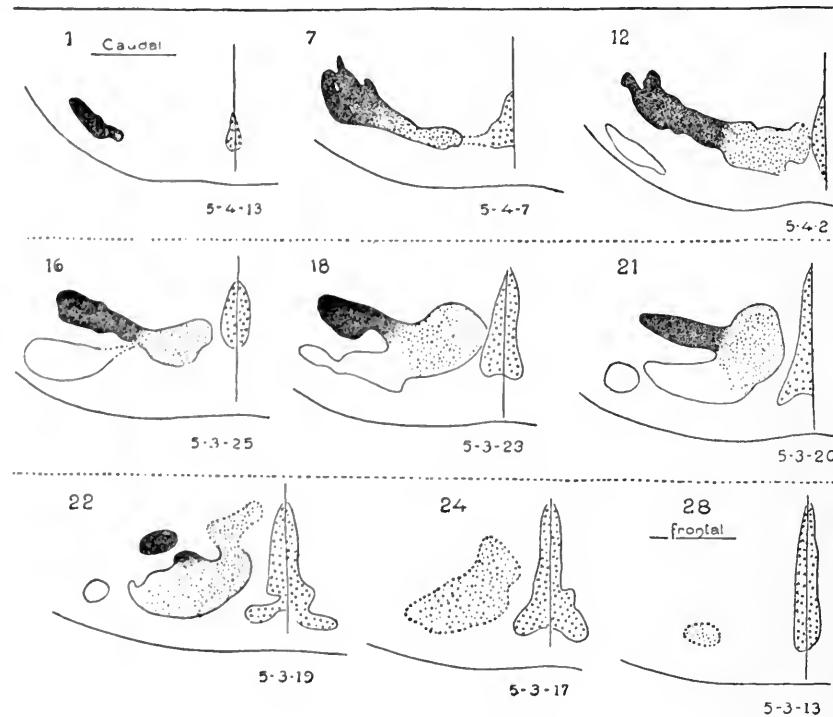


Table 14.
Abbreviated order of sections through the inferior olive of
Lophortyx californicus (*Shaw & Nodd*).
Size of the section = 50 μ . Magnified 20 X.

So we can find a scheme, which holds good with all Birds.

After having discussed the olive of the Mammals, I shall revert to the principal points of it, dealing with eventual homologies of the mammalian olfactory complex.

Now I shall only put some questions about differences and connections between various groups of Birds.

The following questions arise:

Can a classification be made on account of:

- a) the phylogenetic stage;
- b) the size of the birds;
- c) their belonging to the same order;
- d) the function?

Ad a) We know little or nothing about the exact phylogenetic classification of Birds. The Ratitae are very probably the oldest form. Now the most striking thing in Casuaris is the smallness of its ventral lamella and the exclusively lateral accumulation of the cells of that lamella, also the distinct division into a lateral and a medial part of the dorsal lamella.

It would not do, however, to consider for this reason only, the distinct division into a dorso-lateral, medial and ventro-lateral cell-accumulation, to be the primitive type of the avian olive.

Ad b) The small birds certainly do not form a group as opposed to the big ones.

Ad c) But a resemblance between the members of the same order does exist, so the small Palaeornis is very like the big Cacatua and Ara: see the ventral lamella reaching far caudally, the connection of this lamella with the lateral part of the dorsal one in caudal sections, the very striking development of the medial part of the dorsal lamella.

As I do not dispose of several species of other suborders, I cannot trace this question any further.

Ad d) A classification after function is as yet impossible. Some day, when the afferent tracts of the olive and the function, connected with those tracts, will be exactly known, it may be possible to understand the different functions of the birds also by the form of their olives. At present, I cannot find any connection between the various olive-forms and the habits of the birds in question.

Histology.

The *reticular cells* in Birds on the level of the olive, are exactly like those in Fishes: sharp, polygonal, long-stretched. The most frequent forms are the multangular and the long-stretched fusiform ones (figs. 50, 51, 52); the latter very often stand perpendicularly on the raphe (like in Selache maxima).

In big birds, the reticular cells are much larger than those in smaller

ones (c.f. *Casuaris australis*, fig. 50 and *Lophortyx californicus*, fig. 51).



Fig. 50.

Reticular cells of the raphe in
Casuaris australis Wall.
114 X.



Fig. 51.

Reticular cells of the
raphe in *Lophortyx*
californicus
(Shaw & Nodd)
114 X.

Fig. 52 shows the reticular cells in the raphe of *Columba livia domestica neonata*, in silver-stain greatly magnified: in the middle of the long-stretched cell, a round dark nucleus can be seen, surrounded by a lighter coloured „area”.

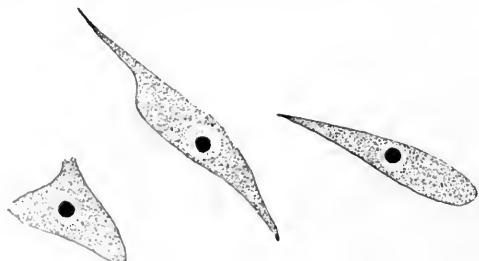


Fig. 52.

Reticular cells in the raphe of *Columba*
livia Bonn. (domest. neon.)

The olive-cells are implanted in a granular substance, analogous with the same substance in Fishes and richly provided with blood-vessels. The cells are rather small, though larger than in Fishes, and pear- or spindle-shaped.



dorsal lamella
(lateral part)

dorsal lamella
(medial part)



ventral lamella
(lateral part)



ventral lamella
(connecting part)

Fig. 53.

Cells of the olive in *Casuaris australis* Wall — 114 X.

Some points can be stated:

1) Big birds have larger cells than smaller ones, c.f. *Casuaris*-
Lophortyx (figs. 53, 54).

2) In caudal sections the cells are scattered rather equally throughout the dorsal lamella.

More frontally, they are chiefly accumulated in:

- the lateral part of the ventral lamella;
- the lateral part of the dorsal lamella;
- the medial part of the dorsal lamella.

In the ventral lamella, the cells are usually more scattered than in the dorsal one.

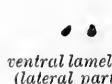
In the dorsal lamella, the cells are most compact in the medial



dorsal lamella
(lateral part)



dorsal lamella
(medial part)



ventral lamella
(lateral part)

Fig. 54.

Cells of the olive in *Lophortyx californicus*
(Shaw & Nodd) — 114 X.

part. In *Cacatua*, however, the cells and nuclei are more oblong, as if they covered the olive and, in consequence of this, are cut longitudinally.



Fig. 58.

Cells of the medial part of the dorsal lamella in *Cacatua roseicapilla* Vieill.
(Situated in the centre of the lamella.)



Fig. 59.

Cells of the medial part of the dorsal lamella in *Cacatua roseicapilla* Vieill.
(Situated at the border of the lamella)

dinarily (figs. 58—59). We shall again find this position in some Mammals (pag. 135).

When comparing the cell-types of the three olive-parts with each other (figs. 53—57), one cannot find any constancy in the differences

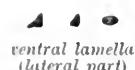
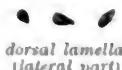


Fig. 55.

Cells of the olive in *Cacatua roseicapilla* Vieill. — 114 ×.



Fig. 56.

Cells of the olive in *Ciconia ciconia* (L.) — 114 ×.

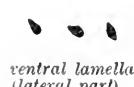


Fig. 57.

Cells of the olive in *Gygnum olor* Gm. — 114 ×.

and resemblances between them. It is the accumulation that makes the difference, not the cell-form.



Fig. 60.

Cells of the lateral part of the ventral lamella in *Columba livia* Bonn.
(*domestica* *neonata*).



Fig. 61.

Cells of the medial part of the dorsal lamella in *Columba livia* Bonn.
(*domestica* *neonata*).

In order to show the details, the olive-cells of *Columba livia domestica* neonata were greatly magnified in the drawings (figs. 60—62). The nucleus of this cell is generally situated in a lighter area.



Fig. 62.
Cells of the lateral part of the dorsal
lamella in *Columba livia Bonn.*
(*domestica* *neonata*).

CHAPTER III.

Mammals.

First I intend to describe casuistically the olives of the various Mammals, I studied.

I examined the following species (Classification of Max Weber, 1904):

Of 1. Monotremata:

Echidna aculeata Shaw.

Of 2. Marsupialia:

Didelphys marsupialis L.

Macropus robustus Gould.

Of 3. Insectivora:

Erinaceus europaeus L.

Talpa europaea L.

Of 4¹). Chiroptera:

Vesperugo noctula (Schreber).

Of 8²). Xenarthra (Edentata):

Tamandua tetradactyla L.

Myrmecophaga jubata L.

Note 1: Of the subclass 5, Galeo-pithecidæ, I had no representative.

Note 2: Of the Edentates I had only some representatives of 8: Xenarthra; Weber divides the Edentata into:

6. Tubulidentata.

7. Pholidota.

8. Xenarthra.

Of 9. Rodentia:

- Lepus cuniculus L.*
Arctomys marmotta L.
Mus musculus L.

Of 11¹). Carnivora (fissipedia):

- Canis familiaris L.*
Felis domestica Brisson.

Of 11b. Carnivora (pinnipedia):

- Phoca vitulina L.*

Of 12. Cetacea (Odontoceti):

- Phocaena communis Brookes.*
Tursiops tursio Fabr.

Of 13. Perissodaetyla:

- Equus caballus L.*

Of 14. Artiodactyla:

- Sus scrofa L. (domesticus).*
Capra hircus L.

Of 21. Proboscidea: ²⁾

- Elephas indicus L.*

Of 22. Sirenia:

- Halicore dugong Erxleb.*
Manatus latirostris Harlan.

Of 23. Prosimiae (Lemuridae):

- Lemur catta L.*

Of 24. Simiae:

- Hapale pennicillatus E. Geoff.*
Oedipomidas ocdipus.
Cebus spce.
Cebus fatuellus.
Ateles hybridus Geoff.
Anthropopithecus troglodytes L.

The olive in Man is generally divided into three parts: a medial and a dorsal one, called accessory olives, and a larger one between these two: the principal olive (also often called: olivary body, German: „Hauptolive”).

I think I have succeeded in finding these parts in all orders of Mammals.

Note 1: 10. Tillodontia are extinct.

Weber has placed the Carnivora before the Ungulata; this, however, has no phylogenetic reason. On the contrary the brain (and also the olive) of Carnivora is often higher developed than that of Ungulates.

Note 2: 15—19 are extinct; of 20, Hyracoidea I had no specimen.

I have tried to avoid the use of new names; as, however, the various parts of the olive in Mammals are not yet named, I was obliged to do so. As I analyse the medial- and the dorsal parts of the mammalian olfactory complex with the accessory olives in Man, I have kept those names, with the omission only of accessory, as being too long for use and incorrect for the majority of Mammals.

So, speaking of: medial and dorsal olive, I have called the analogy of the principal olive in Man: ventro-lateral olive, as the epithet „principal” is incorrect for this little part of the nucleus in most Mammals and the chosen name is a mere descriptive one, like those of the other parts.

As it is, however, confusing, often to repeat the words: lateral, ventral etc. in one sentence, I still sometimes used the name: principal olive.

The first representative of Mammals cannot be put in the usual mammalian scheme without further explanation.

At the end of the chapter, however, when I shall compare the olive of Birds with that of Mammals, I can perhaps throw more light on the interpretation of the oliveform in *Echidna aculeata*.

I shall again begin by giving casuistical descriptions.

Monotremata.

Echidna aculeata Shaw. — Waxreconstruction: Figs. 63, 64, 65, 66, 67, Table 25.

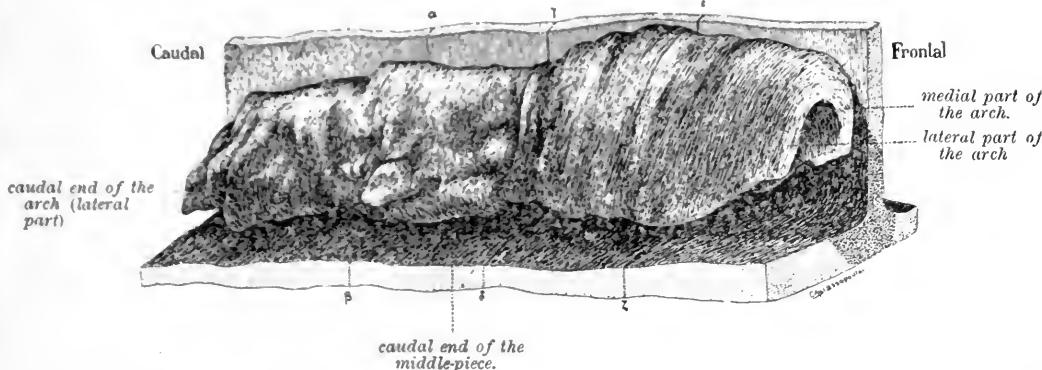


Fig. 63.

Inferior olive of *Echidna aculeata* Shaw. — 18 X (lateral view).

Much to my regret, the material for my study of this animal was not very satisfactorily stained, as it had first been preserved in formaline for a long time, and afterwards in alcohol.

Yet the model, given here, is fairly trustworthy.

It shows that, described roughly, the olive consists of an arch, which,

laterally, dorsally and medially, surrounds an almost round middle-piece (figs. 63—67).

The descriptions of Kölliker (1901) and Ziehen (1908), are conformable to this.

The lateral part of the arch begins a little more caudally

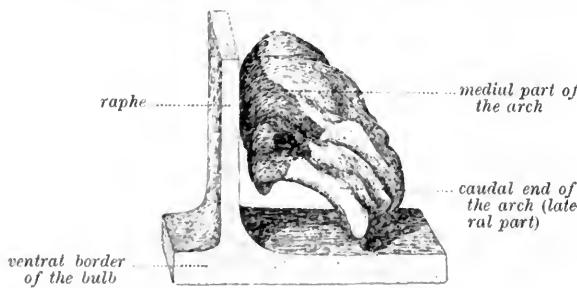


Fig. 64.

Caudal end of the olive in *Echidna aculeata* Shaw.

than the medial one (figs. 63, 64); soon, however, the rounded lamella is complete. Speaking generally, the arch does not change further in its caudo-frontal course. More frontally, the middle-piece appears, which is connected with the lateral part of the arch in many sections (figs. 63, 65; Table 25, s. 32); in a few sections it seems to be free, in others, to be connected with the medial part; absolute certainty, however, could not be attained in this case. At any rate, when we follow it from caudal to frontad, the middle-piece seems to shift a little medially, at the same time growing.



Fig. 65.

Piece of the olive in *Echidna*, between the planes of section $\gamma\delta$ and $\zeta\zeta$. (caudal view).

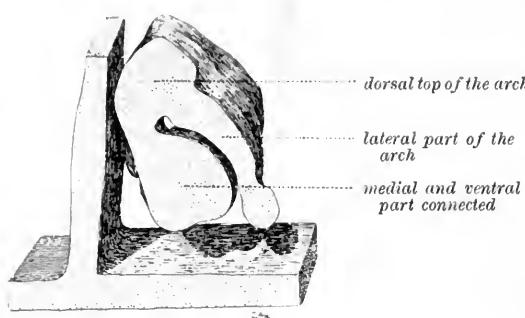


Fig. 66.

Most frontal piece of the olive in *Echidna* (caudal view).

Still more frontally, it is in most sections connected with the medial part of the arch (fig. 66, Table 25, s. 70).

In some sections, it

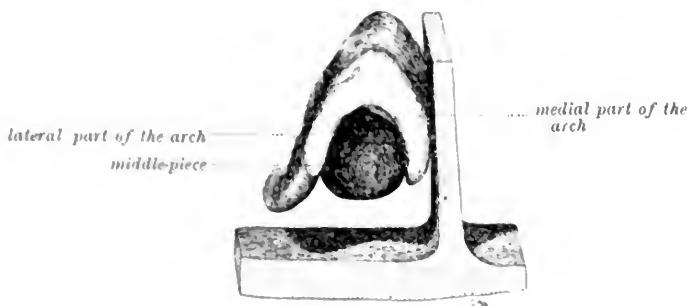


Fig. 67.
Frontal top of the olive in *Echidna* (frontal view).

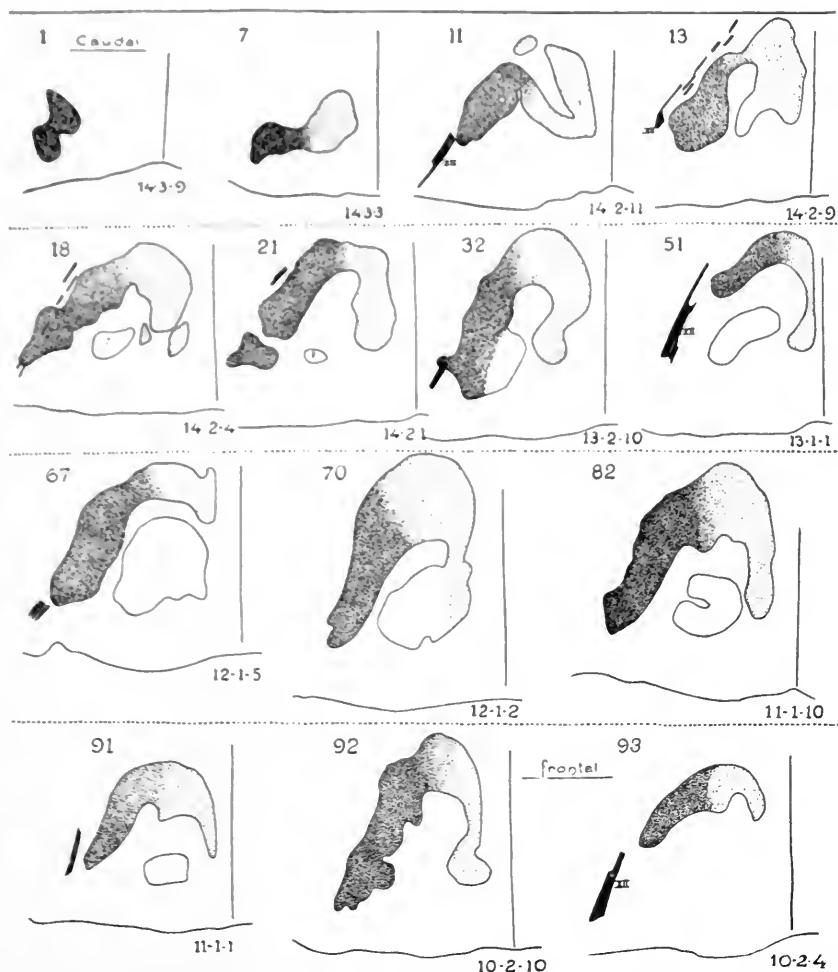


Table 25.

Abbreviated order of sections through the inferior olive of *Echidna aculeata* Shaw.
Size of the section = 50 μ . Magnified 20 X

seems to be free, while in this case the medial part of the arch is very thin or ends dorsally of the large middle-piece, the frontal top of which is quite free.

The arch reaches a little more frontally (figs. 63, 67).

Marsupialia.

Didelphys marsupialis L. — Waxreconstruction: Fig. 68, Table 26.

The medial- and the dorsal olive begin caudally on the same level. The *medial* one at first lies more ventrally; soon, however, it extends

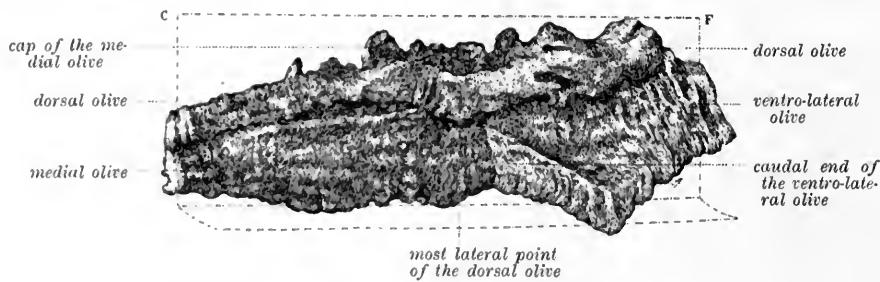


Fig. 68.

Inferior olive of *Didelphys marsupialis* L. — 32.6 X (lateral view).

medially, so that, described roughly, it occupies the angle between raphe and ventral border of the bulb.

The *dorsal* olive lies close to the medial one, both olive-parts being not clearly separated, but united now and then by bridges of grey substance (Table 26, s. 11, 24).

The dorsal one shifts a little laterally, exactly caudally of the beginning of the principal olive (fig. 68).

A little frontally of the middle of the olive-length, a lateral outgrowth appears, which is only slightly separated from the medial part and which corresponds to the *principal olive* in higher Mammals.

The dorsal olive then regains its dorsal position like in the caudal sections and lies in a plane, more parallel to the border of the bulb; its medial end is never separated from the ventro-lateral olive.

In most sections, the medial and the ventro-lateral (or principal) olive forms one undivided complex, of which the medial part probably corresponds to the medial olive of higher Mammals. In most frontal sections, no different parts can be discerned¹⁾.

Note 1: In his specimen, Kankeleit (1913) could distinguish the three parts more plainly: medial and dorsal olive and between them the ventro-lateral one, also with a hilus in the latter. My specimen, being very young, was perhaps for that reason not yet sufficiently developed to show those peculiarities.

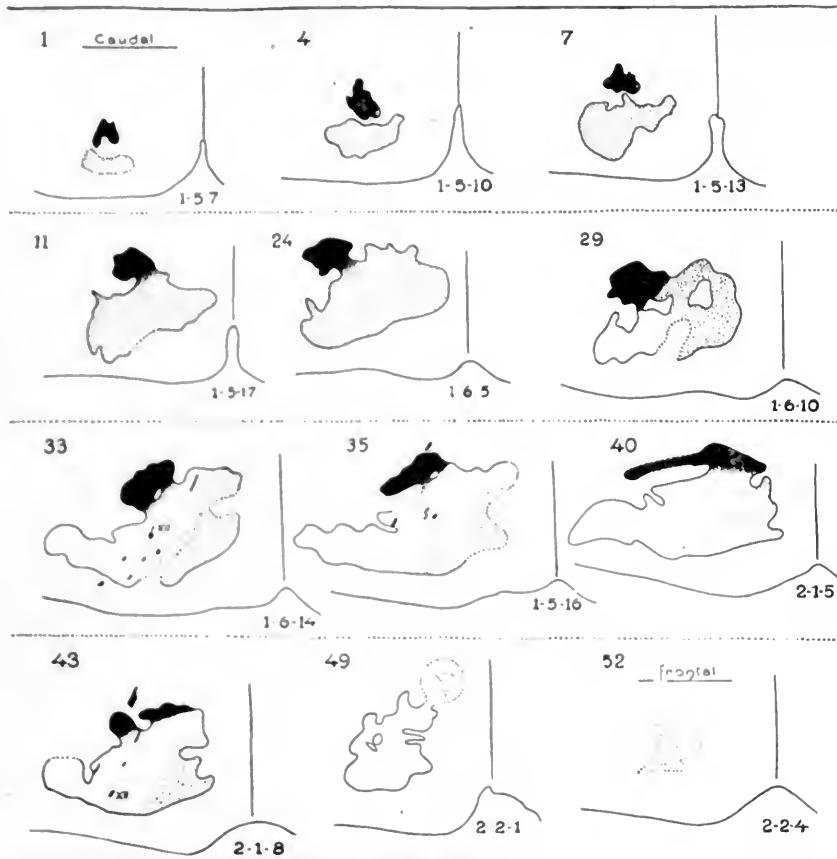


Table 26.

Abbreviated order of sections through the inferior olive of *Didelphis marsupialis*. L.
Size of the section = 50 μ . Magnified 20 \times

Macropus robustus Gould. — Waxreconstruction: Fig. 69, Table 27.

The medial and the dorsal olives appear caudally on the same level, the latter soon migrates laterally and in many sections, remains in this lateral position; the medial olive soon extends medially and shows a groove on its ventral surface (indicated by a in the Table). At the caudal appearance of the principal olive (at about the middle of the olive-length), the dorsal one retakes its medial position, laying itself like a plate on the dorsal lamella of the principal olive, in a plane, more parallel to the ventral border of the bulb, than below.

The three olive-parts, dorsal, ventro-lateral and medial, are on that level united at their dorsal top (Table 27, s. 33—36.).

The form of the dorsal olive shows a *V-figure* in the model, as was also the case with *Didelphys*; in the animals which have still to be described, this V-figure is much clearer.

The dorsal olive is in all sections connected with the lateral lamella of the principal olive, the hilus between these two parts opens laterally and is distinctly visible. In most frontal sections, only the medial part of the dorsal olive remains.

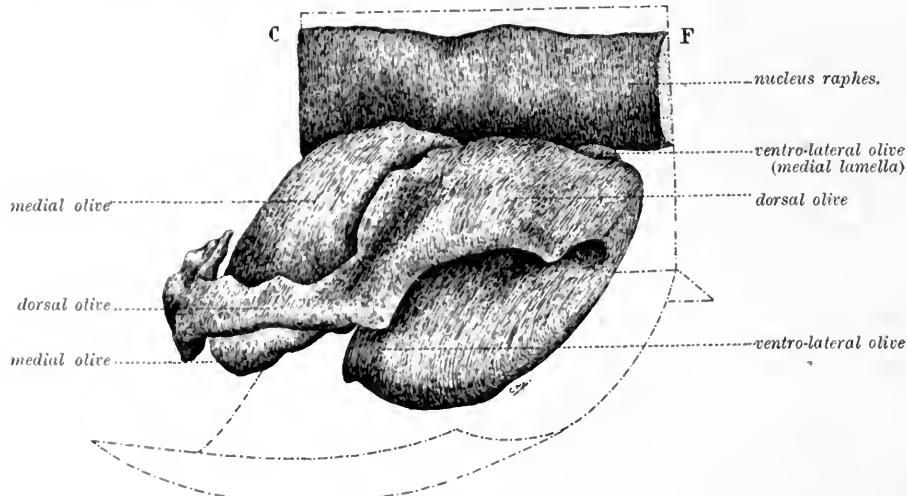


Fig. 69.

Inferior olive of *Macropus robustus* *Gould.* $\pm 20 \times$ (frontal and lateral view).

From the first caudal appearance of the ventro-lateral olive, until its frontal end, the medial one is gradually confined to its most medial part and disappears a few sections below the frontal olive-top.

It is only insufficiently separated from the ventro-lateral olive, best of all in frontal sections by a ventral groove.

The *ventro-lateral* (or *principal*) olive extends farther laterally than the medial one did in the caudal half. Caudally it shows only a dorsal lamella, more frontally, also a ventral lamella frees itself from the medial olive and a hilus, which opens medially, becomes visible. So in frontal¹ sections through the olive of *Macropus robustus*, the „Vierblättertypus” of Kankeleit is visible (Table 27, s. 45—54). I shall afterwards revert to this type, I only wish to draw the attention to the fact, that it can only be seen in the minority by far of the sections through the olive. The medial hilus disappears in higher sections; the medial

Note 1: By frontal is meant the opposite of caudal.

parts of the principal and dorsal olives with the above-mentioned lateral hilus between them, form the frontal end of the inferior olive.

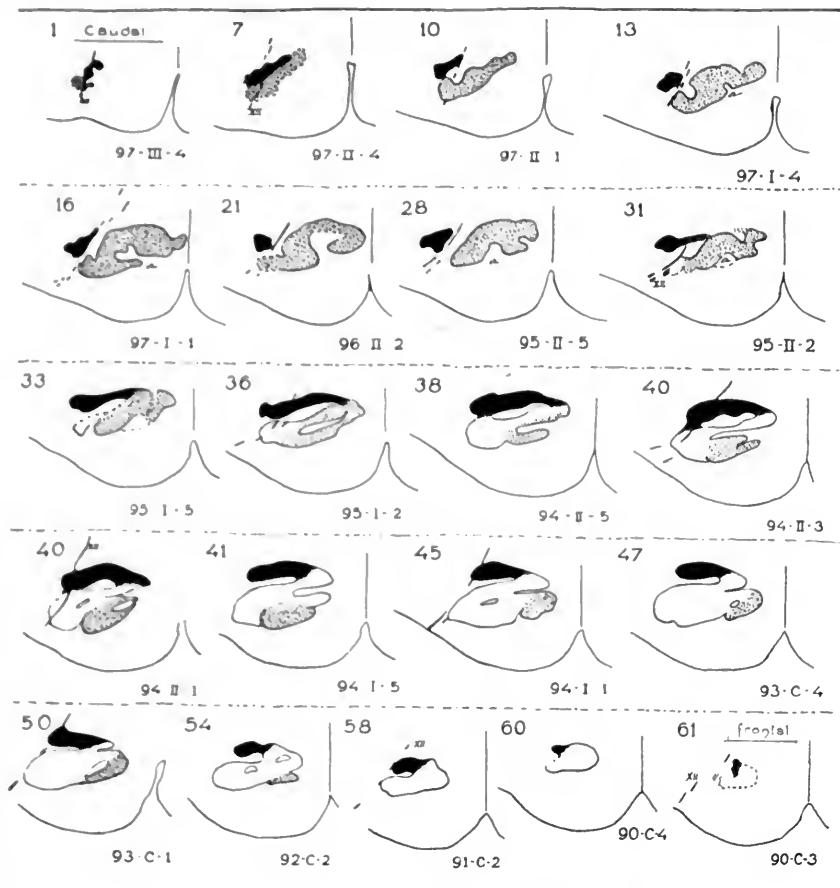


Table 27.

Abbreviated order of sections through the inferior olive of *Macropus robustus* Gould.

Size of the section = 60 μ .

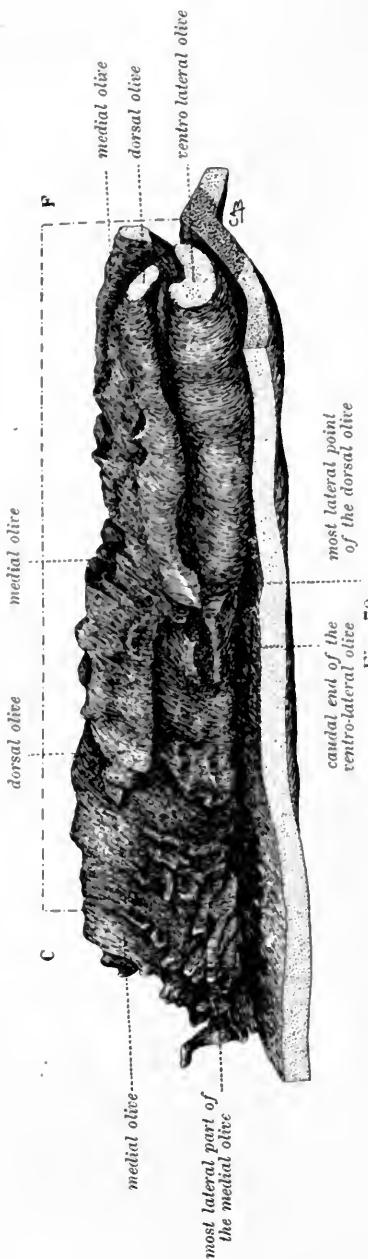
Magnified $\pm 6 \times$.

Insectivora.

Erinaceus europaeus L. — Waxreconstruction: Fig. 70, Table 28.

Described roughly, the *medial olive* lies triangularly between the raphe and the ventral border of the bulb (Table 28, s. 18).

Its most lateral part is rather indistinct. In lower Mammals, like in Fishes and Birds, the borders of the olive are not quite even; small projecting parts extend in various (as a rule: lateral) directions.



Inferior olive of *Erinaceus europaeus* L. — 27 X (frontal and lateral view)

Fig. 70.

The dorsal olive appears at about section 26 (there being 84 in all), closely connected with the medial one.

I considered it to be the dorsal olive, on account of its being projected on the dorso-lateral surface of the medial olive; more-over, its dorsal end is free and separated from the other olive by small fibre-masses (Table 28, s. 34, 41). Last not least, its form is analogous with the dorsal olive of higher Mammals (see Conclusions, pag. 127). About midway the length of the olive, the *ventro-lateral* part appears, extending not far laterally, but occupying the place of the medial olive. Of the latter, only the medial part remains, apparently unto the end.

When the *ventro-lateral* olive appears caudally, the dorsal one shifts dorsally. In Mammals, the dorsal top of this olive-part usually becomes connected with the dorsal lamella of the *ventro-lateral* olive.

In *Erinaceus*, however, this dorsal top is free, while the place of connection is found more ventrally. In this respect, the dorsal olive-part in *Equus* resembles that in *Erinaceus* (compare Table 28, s. 49—55, with Table 43, s. 173—177, pag. 95).

Only on a frontal level (and in very few sections, see fig. 70, Table 28, s. 63—74) the division into three separate olive-parts is rather distinct. In *Erinaceus*, the opening, seen in section 63, perhaps corresponds to the medial hilus in other Mammals.

Talpa europaea L. — Waxreconstruction: Fig. 71, Table 29.

The medial olive appears a few sections more caudally than the dorsal one.

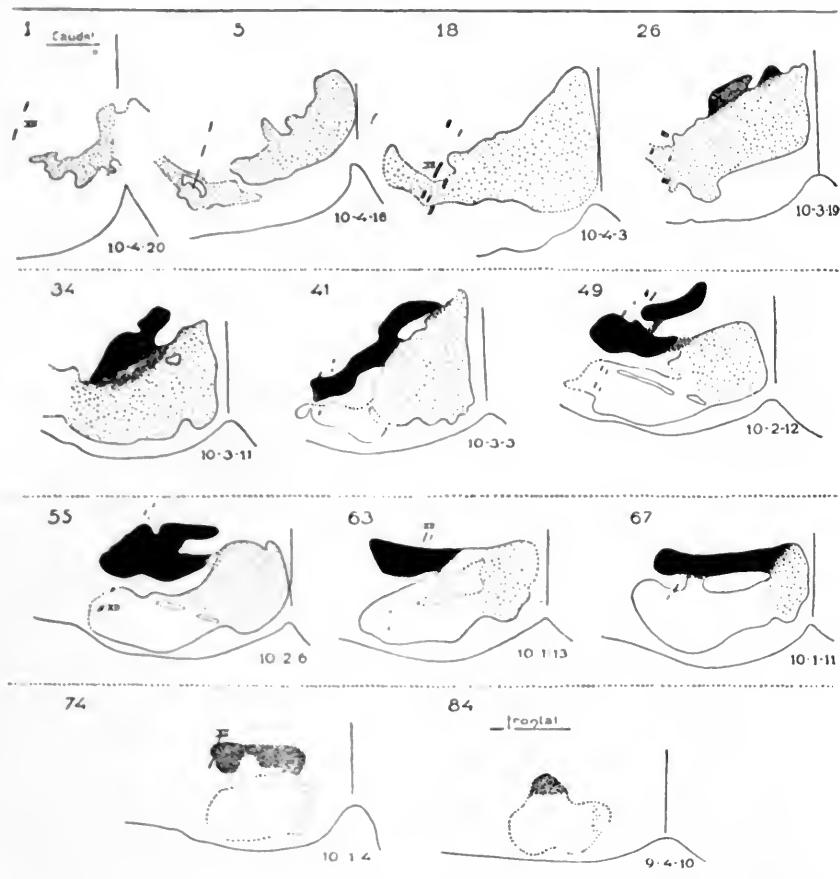


Table 28.

Abbreviated order of sections through the inferior olive of *Erinaceus europaeus*, L.

Size of the section = 30 μ .

Magnified 20 \times .

It soon extends medially, its medial part then bends dorsally and a little laterally, so that a "cap" is formed (model fig. 71, Table 29, s. 16).

The dorsal olive, which had meanwhile migrated ventro-laterally, again turns medially, acquiring a flat form, at the caudal appearance of the principal olive (s. 19 and 21, see also the V-shape in fig. 71).

The ventro-lateral or principal olive appears in section 19, (there being 39 in all) at the ventro-lateral point of the medial olive, as is the case with this part in all Mammals, hitherto described.

A little more frontally, it is almost free from the other parts and extends rather far laterally.

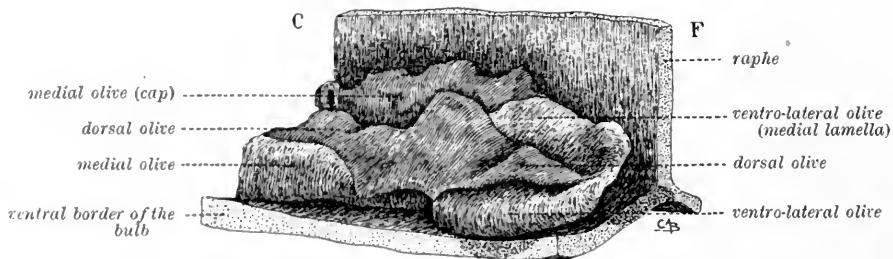


Fig. 71.
Inferior olive of *Talpa europaea* L. — 27.5 X (lateral and frontal view).

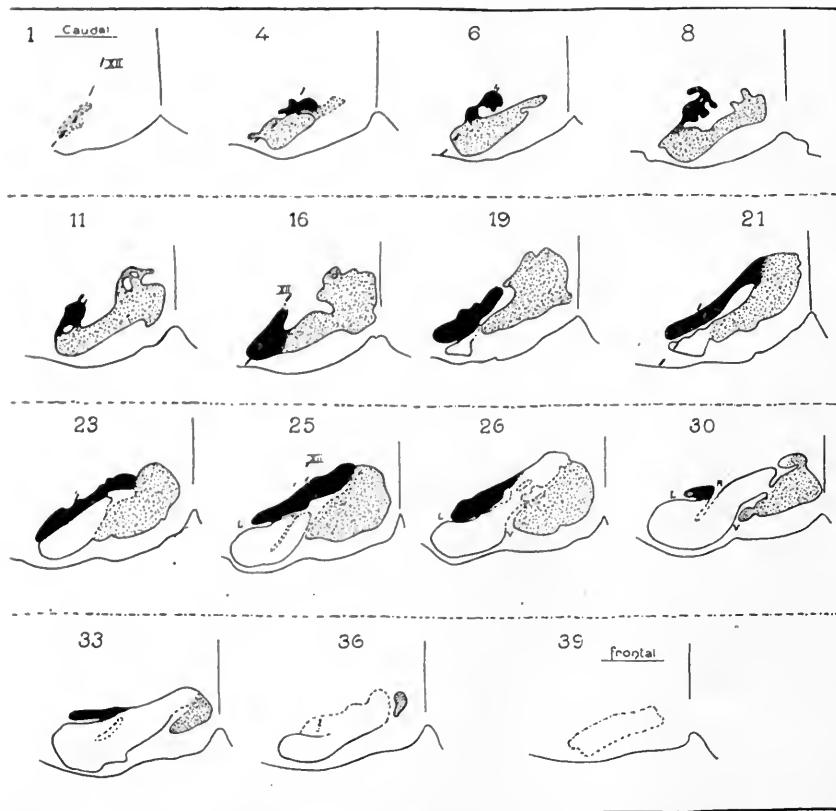


Table 29.

Abbreviated order of sections through the inferior olive of *Talpa europaea* L.

Size of the section = 50 μ . Magnified 20 X.

Soon the medial hilus¹⁾ appears, the lateral lamella is then connected

Note 1: By the characters L, M and V (Table 29) is meant:

L = lateral hilus (between dorsal and principal olive).

M = medial hilus (between the two lamellae of the principal olive).

V = ventral hilus (between medial and principal olive).

with the dorsal olive, the larger ventral one with the medial olive ("Vierblätterform", sections 30 and 33). Only in the most frontal sections, the hilus cannot be ascertained, the dorsal and the ventro-lateral olive in these sections form one undivided complex (Table 29, s. 36, 39).

Of the medial olive, only the most medial part remains, almost until the frontal end (s. 36).

Chiroptera.

Vesperugo noctula (Schreber) (not modelled) — Table 30.

The *medial* and the *dorsal* olives appear at the same caudal level, the latter is not sharply defined, as is the case with nearly all Mammals.

The ventral part of the *medial* olive is the first to appear in caudal sections and shows a little curvature on its ventral surface; soon also

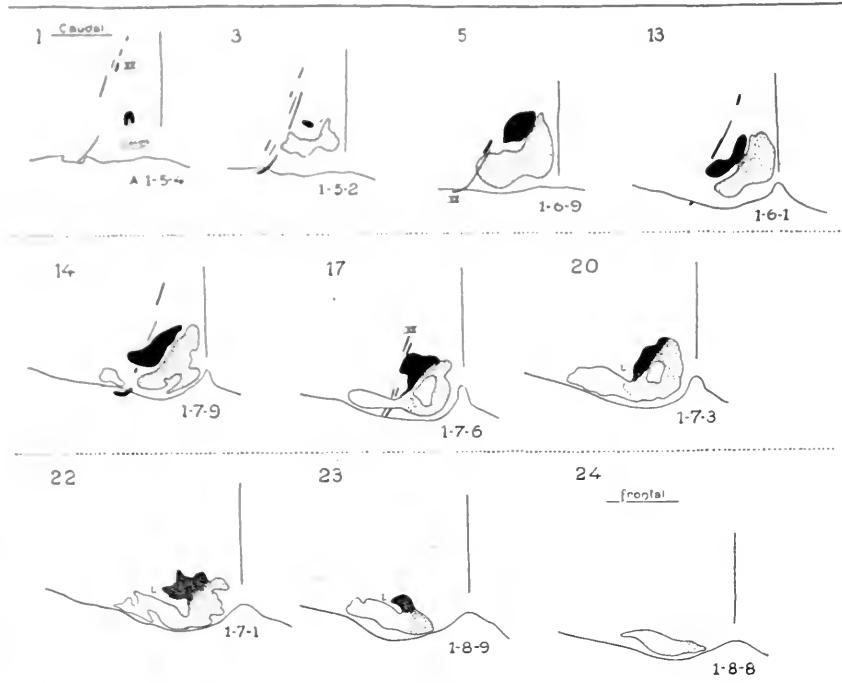


Table 30.

Abbreviated order of sections through the inferior olive of *Vesperugo noctula* (Schreber).
Magnified 20 ×

the medial component is visible. These two components, the ventral and the medial one, can be found over the caudal half of all medial olives, while the angle between them is more or less obtuse and on higher

levels only the medial component remains. This is, of course, expressed schematically. When the ventral component has disappeared, its place is taken by the medial part of the ventro-lateral olive.

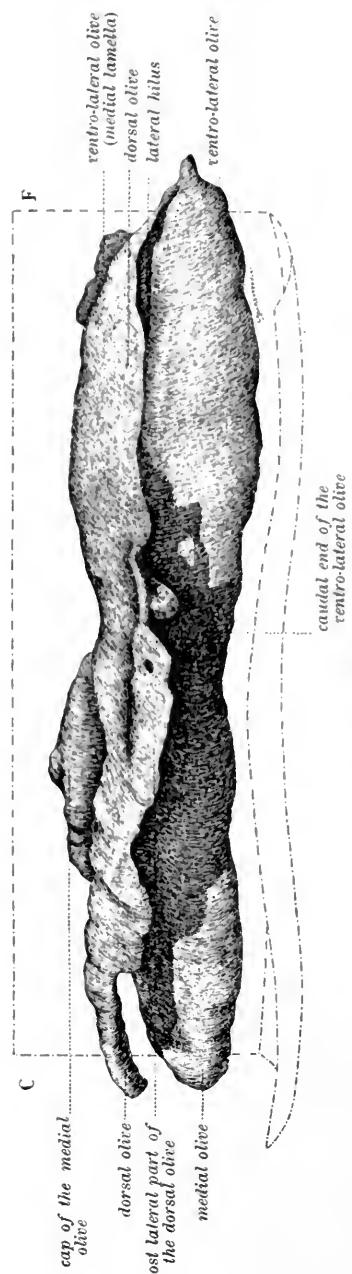


Fig. 72.
Inferior olive of *Tamandua tetradactyla* L. — 14 × (lateral view)

The dorsal olive in *Vesperugo* gradually occupies a more lateral position, again turning dorsally at the appearance of the ventro-lateral (or principal) olive.

The latter is only free at its caudal pole (Table 30, s. 14, there being 24 in all). It is soon connected with the two other parts, which connection grows very close.

The lateral hilus between dorsal and principal olive is very distinct (Table 30, s. 17—23), but it is difficult to distinguish the latter from the medial olive.

The gap, drawn in the sections 17 and 20, probably corresponds to the medial hilus in other Mammals.

Only the most ventral outgrowth extends freely and far laterally. Most frontally, a strand of grey substance remains along the ventral border of the bulb, of which the medial part perhaps belongs to the medial olive.

Rhinolophus and *Pteropus*, which were examined by Kankelweit, seem to show a more distinct "vierblätter" type, with a medial hilus in the principal olive.

Edentata.

Tamandua tetradactyla L. — Wax-reconstruction: Fig. 72, Table 31.

The medial olive is a compact, more or less round, body, although the division into a ventral and a medial component is possible (Table 31, s. 17—36).

On its ventral surface, a rather deep groove is visible which has turned

a little medially in higher sections (Table 31, s. 17—56). The dorsal cap is also present (Table 31, s. 17—36).

The dorsal olive appears at about the same caudal level and gradually shifts laterally.

Characteristic of Edentata is that the dorsal olive lies in a plane which is almost parallel with the ventral border of the bulb, whereas in other Mammals, it lies in a ventro-lateral to dorso-medial plane, forming an angle of about 45° with that border. At the caudal appearance of the principal olive, the dorsal one regains a medial position and becomes connected with the complex of the medial and ventro-lateral olives (Table 31, s. 51).

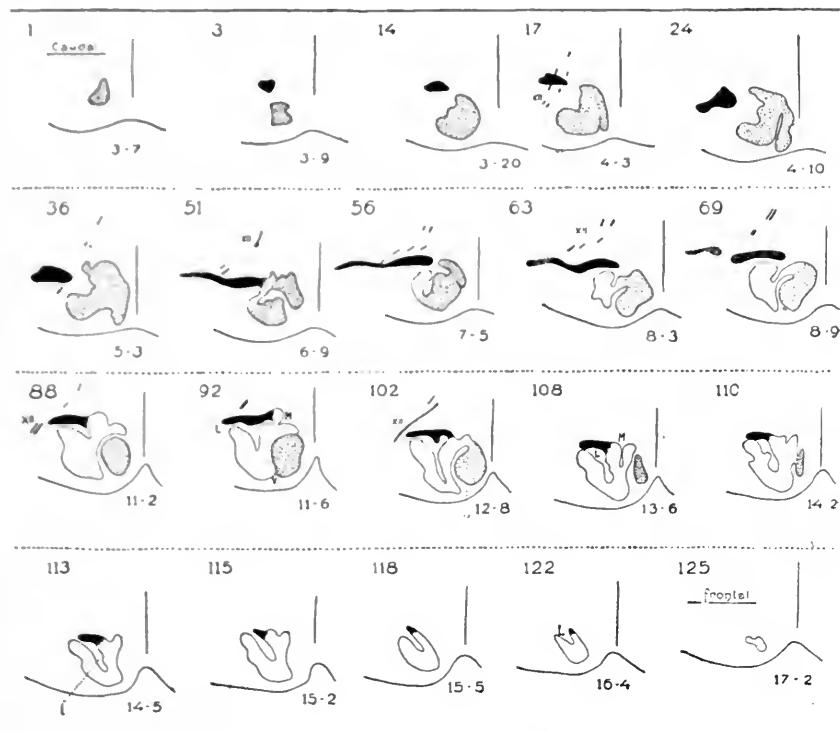


Table 31.

Abbreviated order of sections through the inferior olive of *Tamandua tetradactyla* L.
Size of the section = 60μ . Magnified $\pm 6 \times$.

The ventro-lateral (or principal) olive begins a little caudally of the middle of the olive-length; at first only its dorsal lamella can be distinguished, but soon also its medial one, which in these caudal sections is connected with the medial olive (Table 31, s. 63, 69).

As is also the case with the dorsal olive, the principal one, instead of extending ventro-laterally, bends dorso-laterally. On account of this, the hilus between principal and dorsal olive opens dorso-laterally (Table 31, s. 88 etc.). The medial hilus is only superficial, the fibres do not penetrate deep into it. The dorsal and the principal olive form together the frontal top of the olfactory complex; the medial one ends lower (s. 110).

Myrmecophaga jubata L. — Table 32.

The medial olive has about the same form in *Myrmecophaga* as in *Tamandua*, its ventral groove is still more distinct (Table 32, s. 39—66 indicated by a); the dorsal cap is free from the rest in some sections (Table 32, s. 62).

In higher sections, only its medial part is present.

With regard to the medial olive, the *dorsal olive* extends less caudally than in *Tamandua* (appearing caudally in section 27).

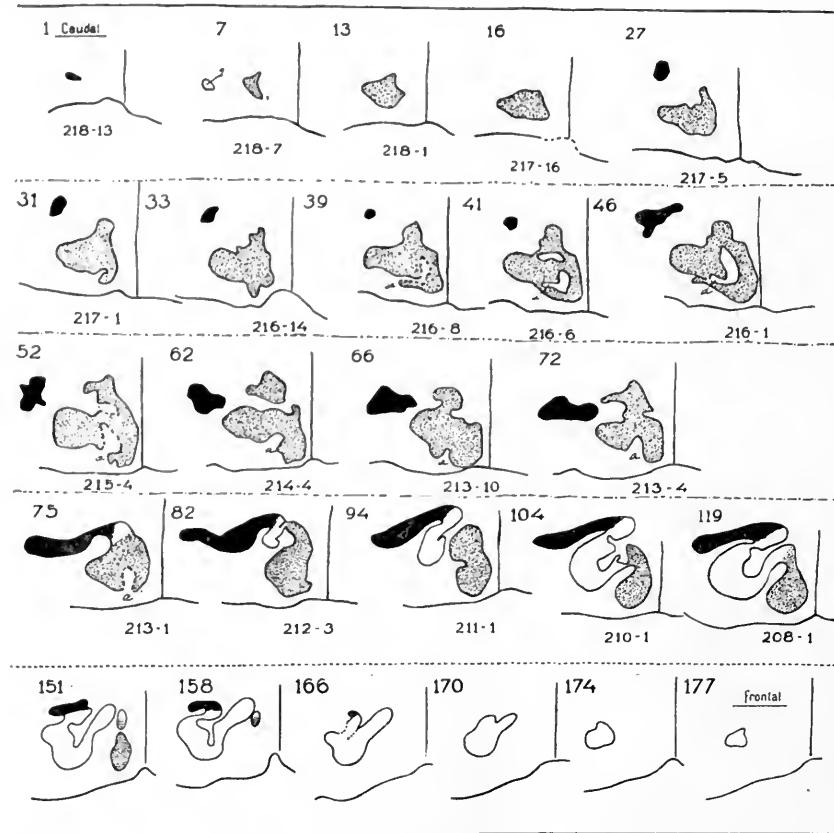


Table 32.

Abbreviated order of sections through the inferior olive of *Myrmecophaga jubata L.*
Size of the section = 60 μ . Magnified $\pm 6 \times$.

Like in all Mammals, its form is nearly round in caudal sections and becomes flat at the caudal appearance of the ventro-lateral olive. For the rest, it does not differ much from the corresponding olive-part in Tamandua, only, frontally, it disappears a few sections lower than in the other Edentate.

Also in this animal, the *ventro-lateral* or *principal* olive is present over the frontal half of the olfactory complex. It shows a more distinct and deeper hilus than in Tamandua and hardly bends dorso-laterally. In the most frontal sections, probably only the principal olive is present.

Rodentia.

Lepus cuniculus. — Waxconstruction: Fig. 73, Table 33.

The whole inferior olive in Lepus is flat, it does not reach far laterally.

The *medial olive* has a smaller medial component than is usually found with Mammals. Only in the very frontal sections, the medial part

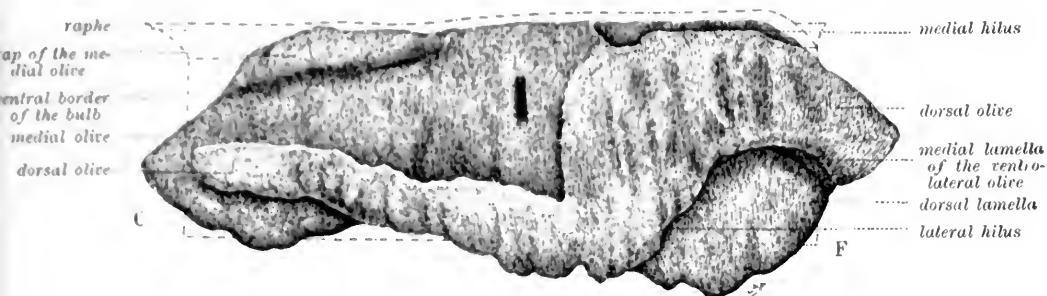


Fig. 73.

Inferior olive of *Lepus cuniculus* L. — 15.75 × (dorsal view).

predominates, the ventral one having disappeared. Over its caudal half, a slight curvature is visible. The dorsal cap is distinctly visible (fig. 73, Table 33, s. 17, 34).

The *dorsal olive* appears caudally at about the same level (Table 33, s. 7), shifting laterally in the next sections; its form is oblong. At the appearance of the principal olive, it again turns medially and acquires a flat form (see the V-shape in the model).

Of the *ventro-lateral* (*principal*) olive, the dorsal lamella reaches more caudally than the medial one (Table 33, s. 44), the medial hilus separating them.

More frontally, this hilus becomes superficial and does not communicate with the fibre-masses between the lamellae (Table 33, s. 55).

The dorsal olive then blocks up the medial hilus and becomes con-

nected with the medial lamella; the dorsal lamella becomes shorter than the medial one and disappears (about s. 64; see also fig. 73).

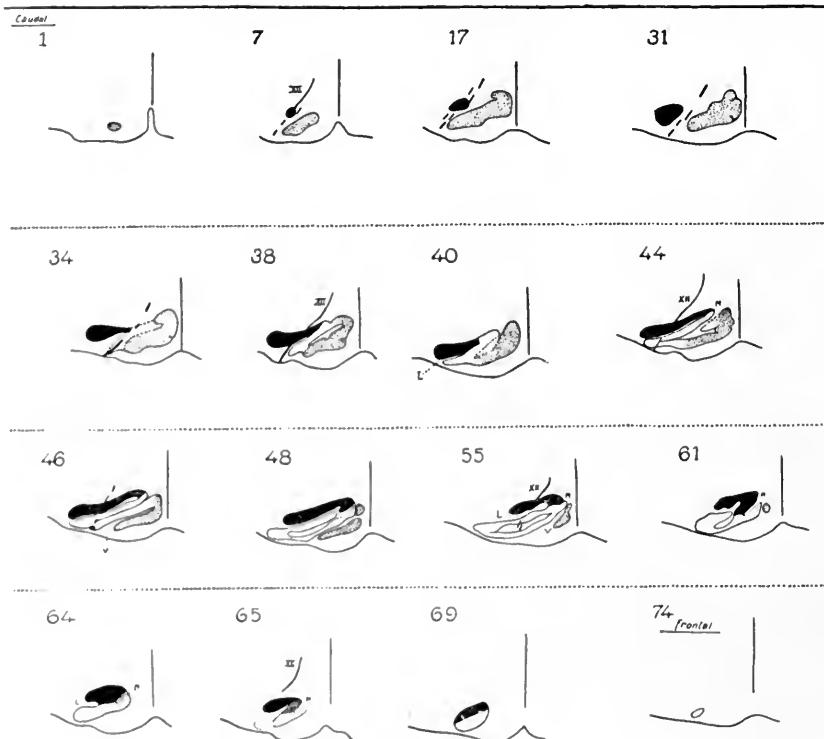


Table 33.

Abbreviated order of sections through the inferior olive of *Lepus cuniculus L.*
Size of the section = 50 μ . Magnified $\pm 6 \times$.

In the remaining sections, one sees the dorsal olive and the ventral lamella of the principal olive gradually decrease and disappear.

Arctomys marmotta L. — Table 34.

The medial olive is present over about the same part of the olive-length as in *Lepus*, resp. over 85 % and 82,5 %.

A division into a ventral and a medial component is hardly possible in *Arctomys*, this whole part, until the frontal end, being situated in one ventrolateral-to-dorsomedial plane. A ventral groove cannot be observed, but the dorsal cap is present (Table 34, s. 14—30).

The dorsal olive already shows its plateform in some sections below the principal olive (Table 34, s. 23); yet, speaking generally, it is no exception to the rule of being compact-oblong caudally, and thin-plate-

shaped frontally of the principal olive (cf. Table 34, s. 30—37 with s. 50—74).

Probably the ventro-lateral (principal) olive already appears in the sections 30—35 (Table 34). More frontally, its dorsal lamella becomes better developed and still more frontally (Table 34, s. 50—56), its medial lamella gets free from the medial olive, with the exception of its dorsal top.

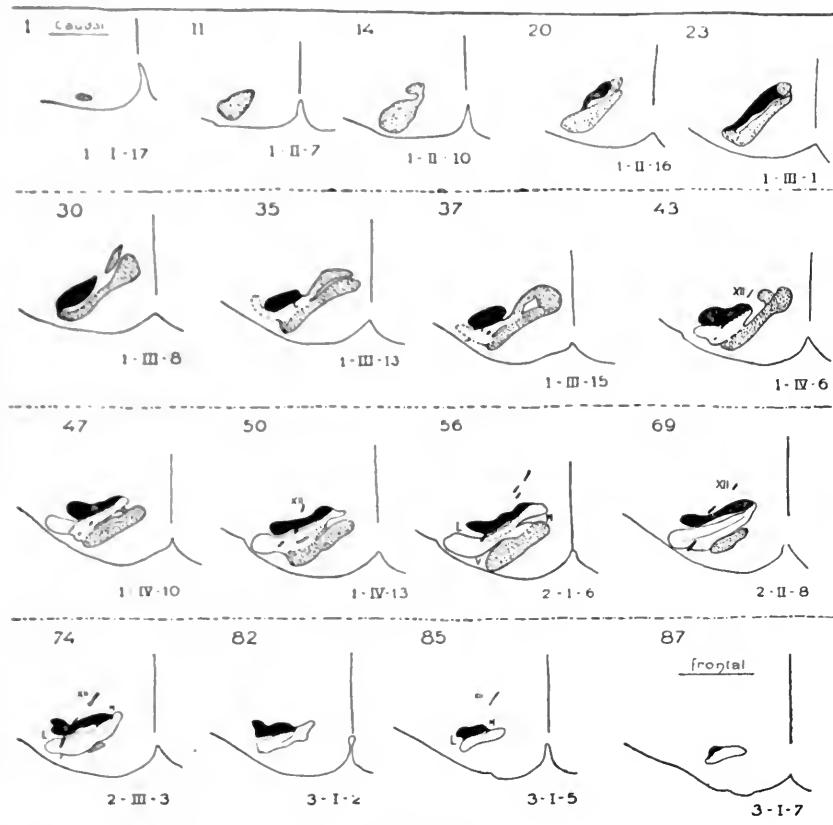


Table 34.

Abbreviated order of sections through the inferior olive of *Arctomys marinotta* L.
Magnified $\pm 6 \times$.

The medial hilus is visible until almost the frontal end, though it is very narrow.

The dorsal olive and the dorsal lamella of the principal olive are directly connected at their dorsal tops.

The two lamellae and the dorsal olive gradually decrease and disappear together.

Mus musculus. — Table 35.

The medial olive is very well-developed. The division into a ventral and a medial component is distinctly visible (Table 35, s. 26—41); the dorsal cap is connected with the medial lamella of the principal olive (Table 35, s. 49); frontally of that section, the medial lamella, which gradually extends dorsally, occupying the place of the cap, bends ventrally into the medial olive (Table 35, s. 52—84).

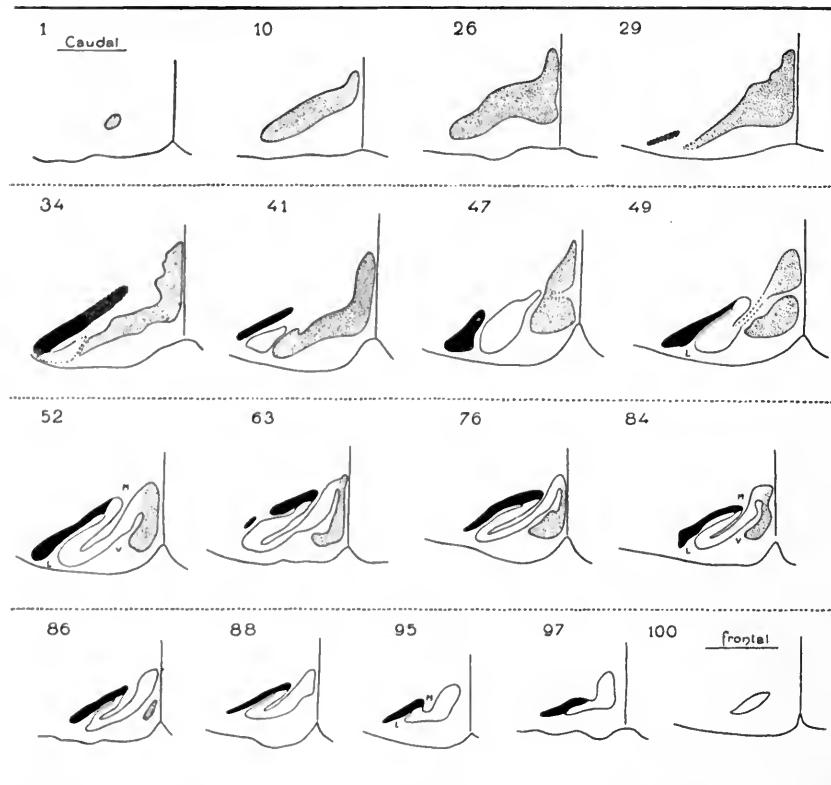


Table 35.

Abbreviated order of sections through the inferior olive of *Mus musculus L.*
Magnified 20 X

In most frontal sections (s. 86), the medial olive is quite free from the other parts.

The dorsal olive is visible only during the presence of the ventro-lateral olive (from s. 41 until the frontal end).

Lower than in section 41 (Table 35), it is very probably present in s. 29—34 (it is still more indistinct in lower sections, so that I was not able to draw it there).

From s. 41 until the frontal end, the dorsal olive presents the usual shape: it is flat and bends into the dorsal lamella of the principal olive.

The ventro-lateral (principal) olive reaches rather far caudally, covering 66% of the entire olfactory complex. The dorsal lamella is developed first. The medial lamella, however, soon becomes more and more important (Table 35, s. 49—100), being the most frontal olive-part (Table 35, s. 97—100).

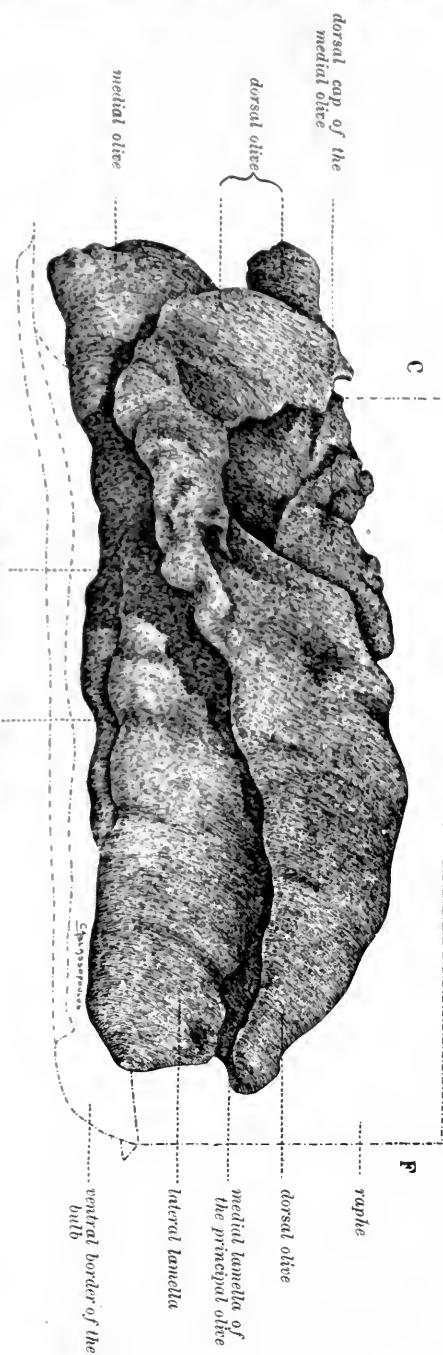
Carnivora.

Canis familiaris L. — Waxreconstruction: Fig. 74, Table 36.

The medial and the dorsal olive appear on the same caudal level.

The medial olive in *Canis* is well-developed; it shows a ventral groove (Table 36, s. 11—17, indicated by a) and a dorsal cap (Table 36, s. 6—21); the division into a ventral and a medial component is not very marked, the total medial olive being placed in a plane, which makes an angle of 45% with the raphe. The medial olive shows an outgrowth, which forms the caudal end of the dorsal lamella of the principal olive. More frontally also

Inferior olive of *Canis familiaris* L. — 45 $\frac{3}{4}$ X (lateral view).



the medial lamella becomes independent of the medial olive, but for its dorsal top (Table 36, s. 26—39).

When cap and outgrowth have disappeared, the rest of the medial olive is again placed in the same plane as it was in caudal sections (see above) and gradually disappears, its medial part extending farthest frontally (Table 36, s. 26—41).

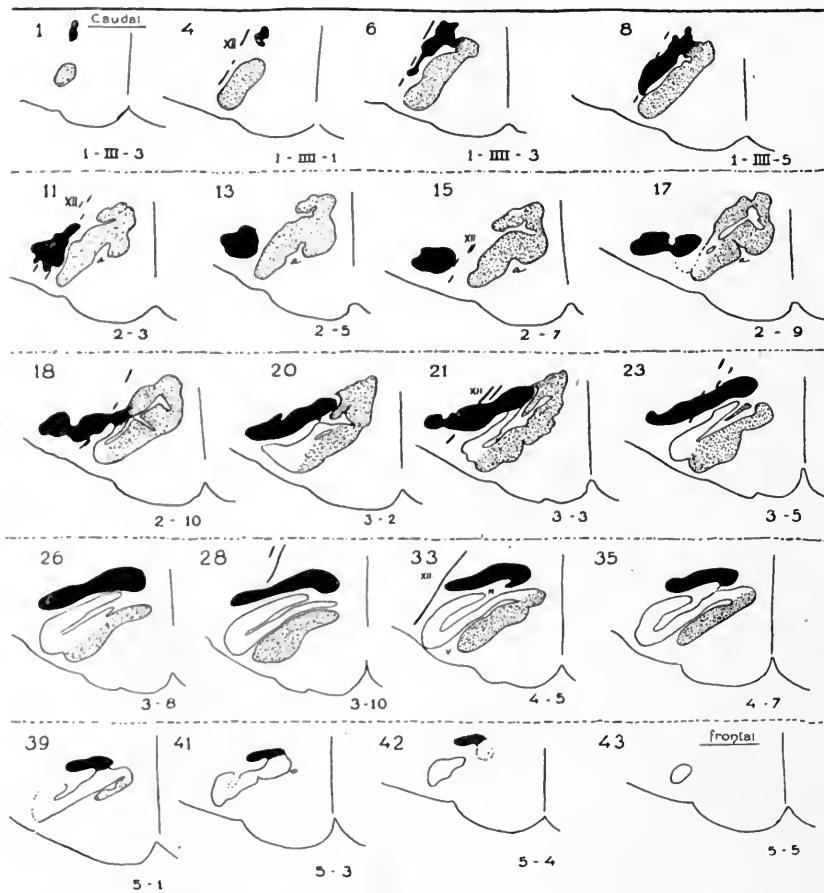


Table 36.

Abbreviated order of sections through the inferior olive of *Canis familiaris L.*
Size of the section = 60 μ . Magnified $\pm 6 \times$.

The dorsal olive, also well-developed, is caudally connected with the cap of the medial olive (Table 36, s. 6—8); more frontally it occupies a very lateral position and again turns medially, when the principal olive appears, thus showing a distinct V-figure (fig. 74).

More frontally, it lies like a plate over the dorsal lamella of the principal olive, while still more frontally it blocks up the medial hilus (Table 36, s. 28—35) and becomes connected with the medial lamella (Table 36, s. 39—42). It reaches almost unto the frontal end of the olfactory complex.

The *ventro-lateral* (or *principal*) olive, when compared with the other parts, is only slightly developed.

It reaches rather far caudally, but is only well-developed over the smaller half of the olfactory system (from section 26 until the frontal end).

Most caudally, only the dorsal lamella is free and developed, more frontally, also the ventral lamella gets loose from the medial olive and grows longer than the dorsal one.

The latter gradually becomes shorter and disappears at about s. 41 (Table 36); the medial lamella, connected with the dorsal olive, reaches most frontally (Table 36, s. 43).

Felis domestica Brisson. — Table 37.

The most caudal to appear is the *medial olive*.

A division into a ventral and a medial component is still more difficult than in *Canis*. In some sections a slight ventral groove is visible (Table 37, s. 21—24).

In the sections of the first (caudal) appearance of the principal olive (Table 37, s. 31—39), a dorsal cap with a ventro-lateral outgrowth can be seen.

When the principal olive becomes more developed, the cap disappears.

As long as the medial olive is present, it is situated in the often mentioned slanting plane, in which it gradually decreases, to disappear below the frontal top of the olfactory complex (Table 37, s. 72).

At its caudal appearance, the *dorsal olive* lies rather dorsally; it soon gets its lateral position (Table 37, s. 21—31) and returns medially when the principal olive becomes visible; it then lies like a plate over the dorsal lamella, while, more frontally, it blocks up the medial hilus (Table 37, s. 54—60) and becomes connected with the medial lamella of the principal olive (Table 37, s. 62—75); it disappears exactly below the frontal top of the olfactory complex (Table 37, s. 77).

Also in the cat, the *ventro-lateral* (or *principal*) olive is only well-developed over the smaller half of the olfactory complex. Most caudally, (Table 37, s. 28—42) only the dorsal lamella is present, more frontally, also the medial one gets loose from the medial olive and soon becomes the most important.

The dorsal lamella gets shorter and disappears first (Table 37, s. 75), while the medial one is connected with the dorsal olive (Table 37, s.

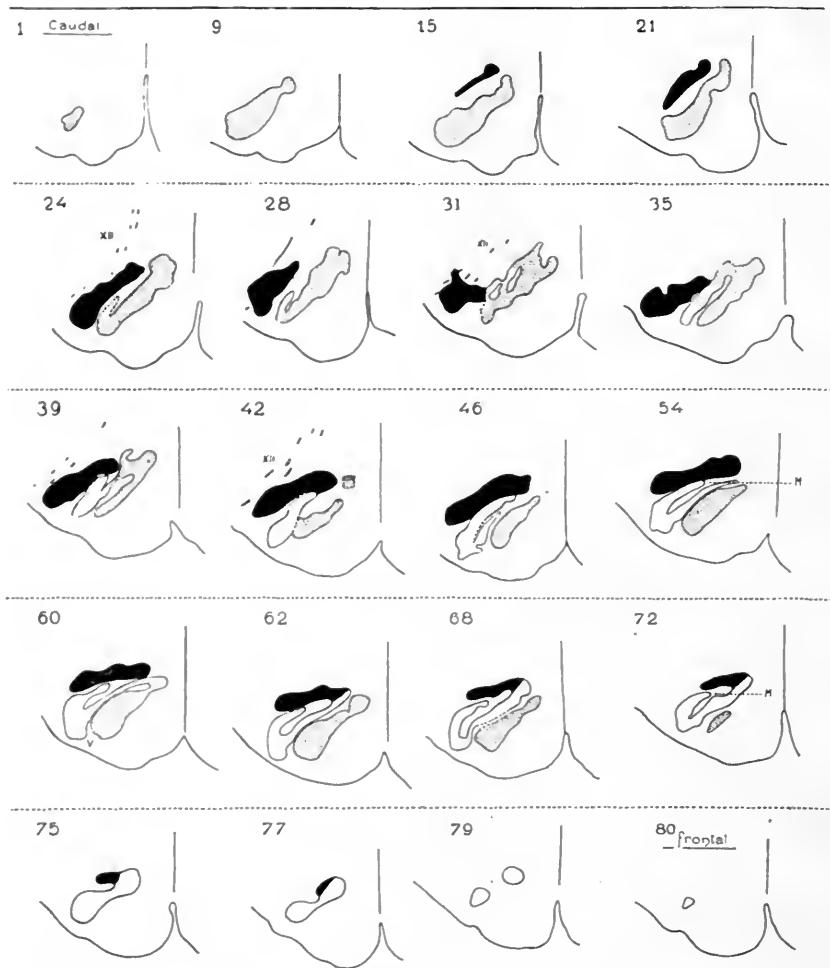


Table 37.

Abbreviated order of sections through the inferior olive of *Felis domestica* Brisson.
Magnified $\pm 6 \times$.

62—77). Like in Canis, it is in most frontal sections divided into a dorsal and a ventral part, of which the latter reaches most frontally (Table 37, s. 79—80).

It will undoubtedly have been observed, that the inferior olive of *Felis domestica* is very like that of *Canis familiaris*.

Pinnipedia.

Phoca vitulina L. — Waxreconstruction: Fig. 75, Table 38.

Most striking in the oliva inferior of *Phoca vitulina* is its compactness¹⁾ in caudo-frontal dimension.

The medial olive is the most caudal part. A division into a ventral and a medial component is possible (Table 38, s. 19—22); the dorsal cap and its outgrowth are visible at the caudal appearance of the principal

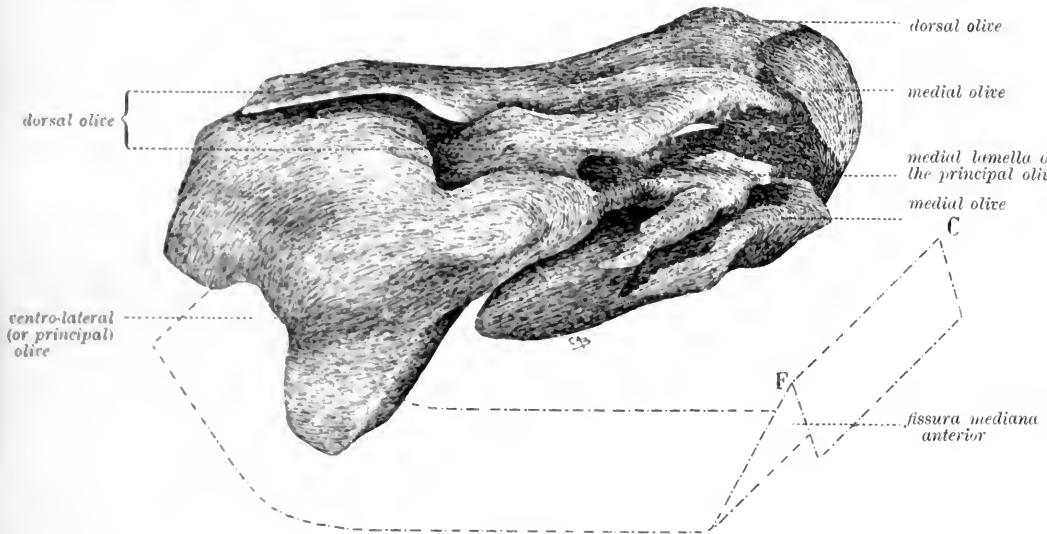


Fig. 75.

Inferior olive of *Phoca vitulina L.* — 15 × (caudal and medial view).

olive. On that level the dorsal and the medial olive are connected (Table 38, s. 22). More frontally, the cap disappears; the medial part of the olive remains, it even becomes larger and ends on a much more frontal level (Table 38, s. 67).

The dorsal olive has the usual dorsal position on a caudal level (Table 38, s. 16); more frontally, it acquires a more lateral position and returns medially at the caudal appearance of the principal olive (Table 38, s. 16—22); over its frontal half it lies like a long thin plate over the dorsal lamella of the principal olive; so the usual V-shape is also seen in this animal.

Most frontally, the dorsal olive blocks up the medial hilus, like in

Note 1: This is in perfect harmony with the fronto-caudal compactness, which is shown in the whole brain (especially the Prosencephalon) of this animal.

Carnivora, but in a different manner, viz. it embraces the dorsal point of the dorsal lamella like a fork (see fig. 75 and Table 38, s. 52), then lies between the two lamellae and is parallel to them (Table 38, s. 58—67). Only in the very frontal sections it becomes connected with the medial lamella (Table 38, s. 70).

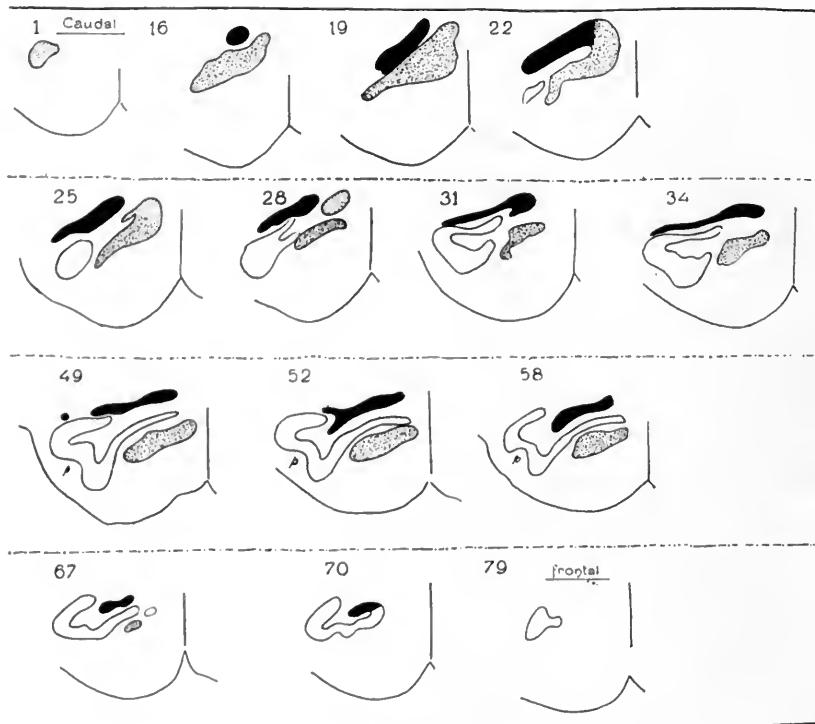


Table 38.

Abbreviated order of sections through the inferior olive of *Phoca vitulina L.*

The ventro-lateral (principal) olive is well-developed, occupying 71% of the total olive-length, which is considerably more than in *Canis* and *Felis*. Like in Carnivora, the dorsal lamella is largest in caudal regions; more frontally, the medial one is more important, while the dorsal lamella becomes shorter. For the first time in the series of Mammals, we find here a distinct sulcus in the principal olive, namely in the connecting part of the two lamellae (Model fig. 75, Table 38, s. 49—58, indicated by p). The dorsal top of the medial lamella becomes independent of the rest and remains present in some sections (Table 38, s. 67), inclining just a little ventrally (like in *Halicore* Table 46, s. 152—164). Speaking generally, the olive of *Phoca*, most of all resembles

that of Carnivora, with the exception of its being so very compact and of some small peculiarities.

Frontally the two lamellae of the principal olive melt together and form the most frontal part of the olfactory complex.

Cetacea.

Phocaena communis Brookes. — Waxreconstruction: Fig. 76, 77, Table 39.

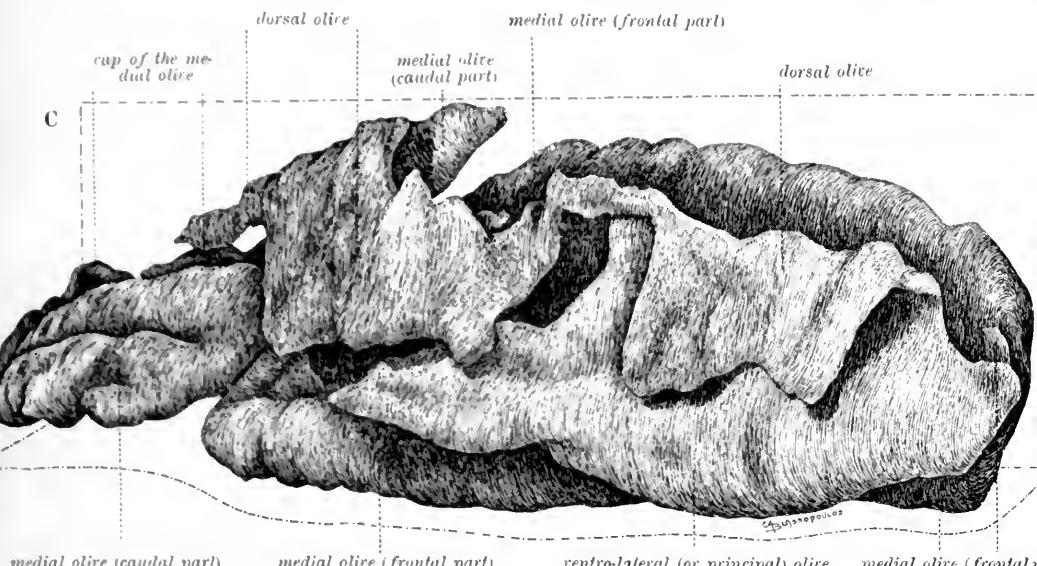


Fig. 76.

Inferior olive of *Phocaena communis Brookes*. — $15\frac{3}{4} \times$ (lateral view).

In *Phocaena*, one is most struck by the enormous development of the *medial olive*.

This can be divided into a caudal and a frontal part, of which the former resembles the medial olive in other Mammals and the latter is most enormously developed.

The caudal part (Table 39, s. 1—25) shows two rather deep grooves, a lateral and a ventral one (cf. fig. 85, pag. 101). We also find a dorsal cap and a ventro-lateral outgrowth, which disappears when the frontal part of the medial olive is fully developed.

This frontal part appears ventrally of the caudal one and pushes the latter dorsally by its strong development (Table 39, s. 16—25). In caudal sections it has a lateral curvature, but more frontally it is quite smooth and rounded; only in still more frontal sections a groove is present, caused by the widening of the base (Table 39, s. 50; more

pronounced in *Tursiops* Table: 40, s.127—221). Its form resembles a wedge, the dorso-ventral dimension being the largest. Frontally it rapidly diminishes and disappears at the same level as the principal olive. The two

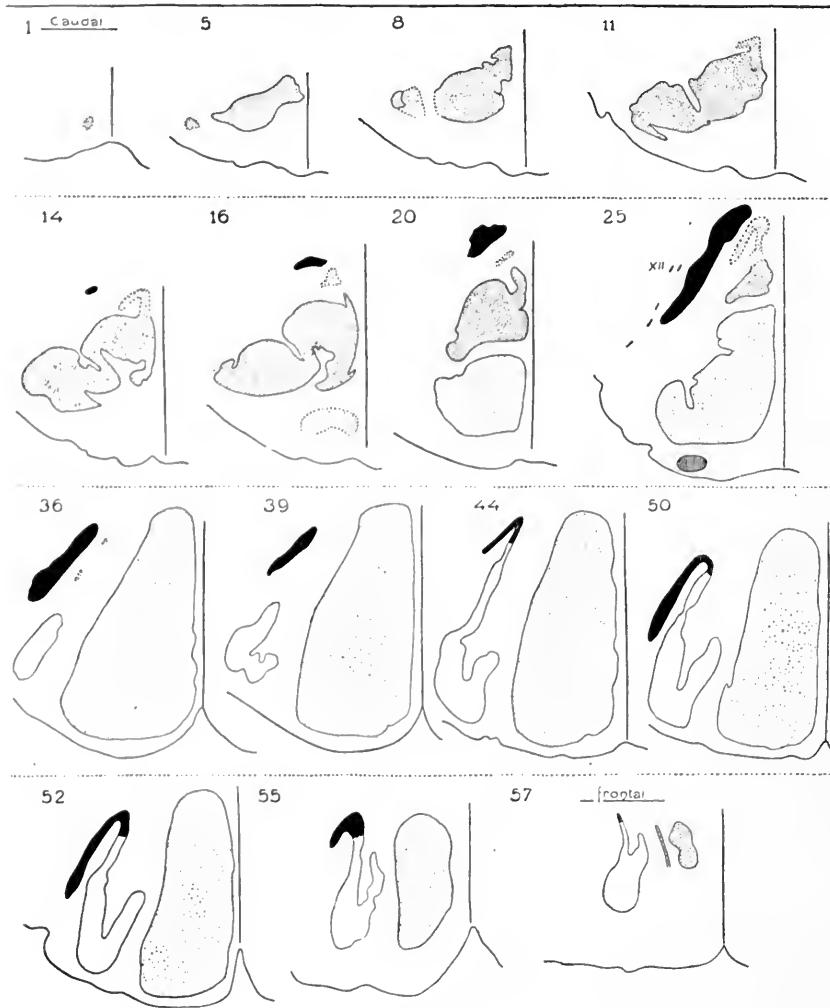


Table 39.

Abbreviated order of sections through the inferior of *Phocaena communis* Brookes.
Size of the section = 500 μ .

parts of the medial olive, situated caudo-dorsally and frontally (the model was seen from medially throughout the raphe), are best shown in fig. 77.

The dorsal olive is rather poorly developed.

In caudal sections it lies dorsally of the medial olive, while more

frontally it has a lateral position, returning dorsally at the caudal appearance of the principal olive. On that level it is over a short distance badly represented¹⁾, showing a large ventral gap in the model (fig. 76, Table 39, s. 44).

Most frontally it bends into the dorsal lamella of the principal olive and probably forms its dorsal top.

The ventro-lateral (or principal) olive is poorly developed, when compared with the medial one; it distinctly shows, however, two lamellae and is free from other olive-parts. The dorsal lamella is developed best, though perhaps its length seems longer than it really is, by its prolongation with the dorsal olive. It reaches most frontally, together with the large part of the medial olive.

Tursiops tursio Fabr.
Table 40.

The olive of *Tursiops* resembles that of *Phocaena* very much.

The medial olive can also be divided into a caudal part and a larger frontal one, of which the caudal part shows the grooves, mentioned in *Phocaena*, which will also be described in *Halicore*.

Note 1: Speaking generally, it is less distinct over its frontal half than over its caudal one.

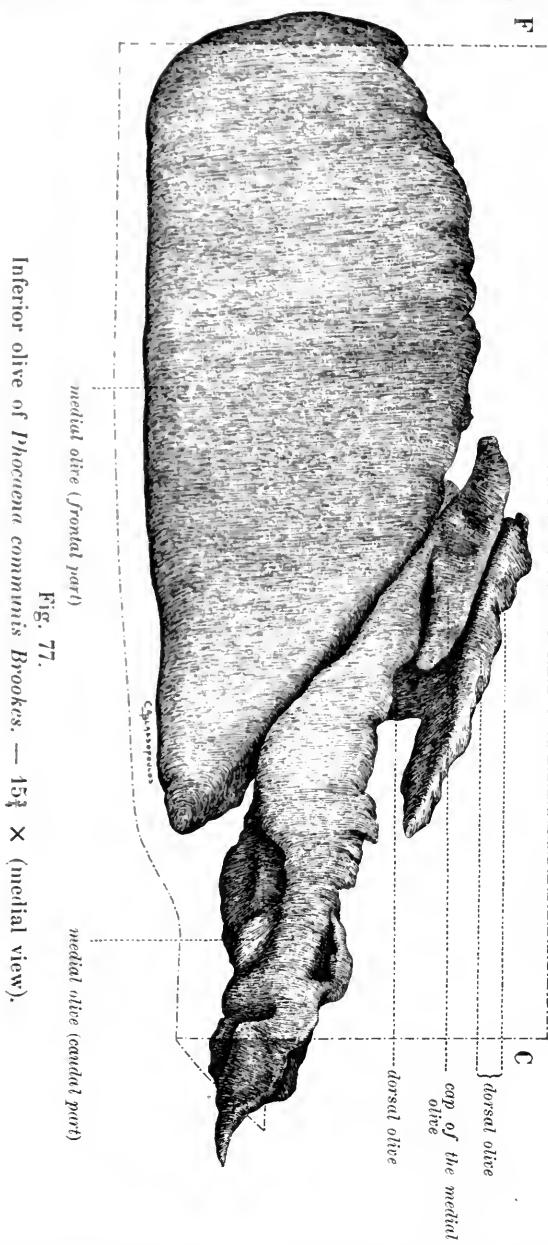


Fig. 77.

Inferior olive of *Phocaena communis* Brookes. — 15 $\frac{1}{4}$ X (medial view).

More frontally the lamiella, ventral of the lateral groove, gets free, decreases and becomes connected with the large frontal part of the medial olive (Table 40, s. 53—71).

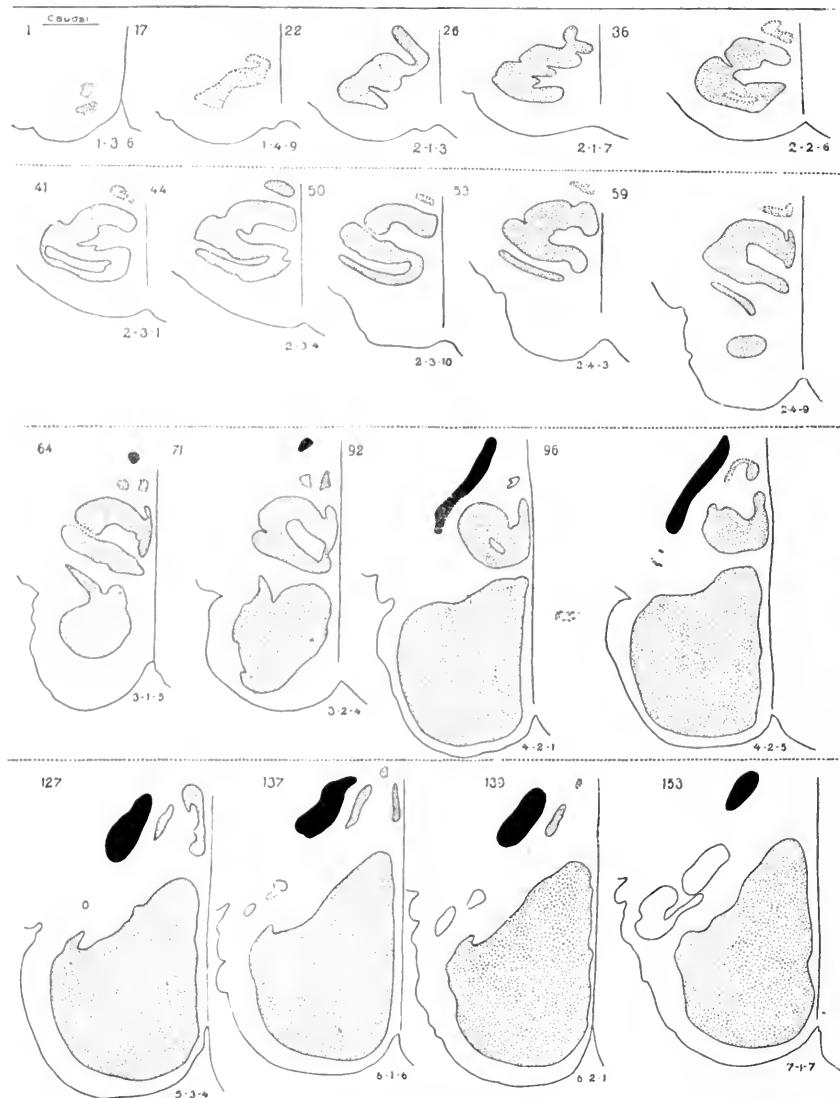


Table 40.

Abbreviated order of sections through the inferior olive of *Tursiops tursio* Fabr.
Magnified 2.5 X

The rest of the caudal part loses its grooves and becomes compact (Table 40, s. 64—96), while it is pushed dorsalward by the enormous development of the frontal part.

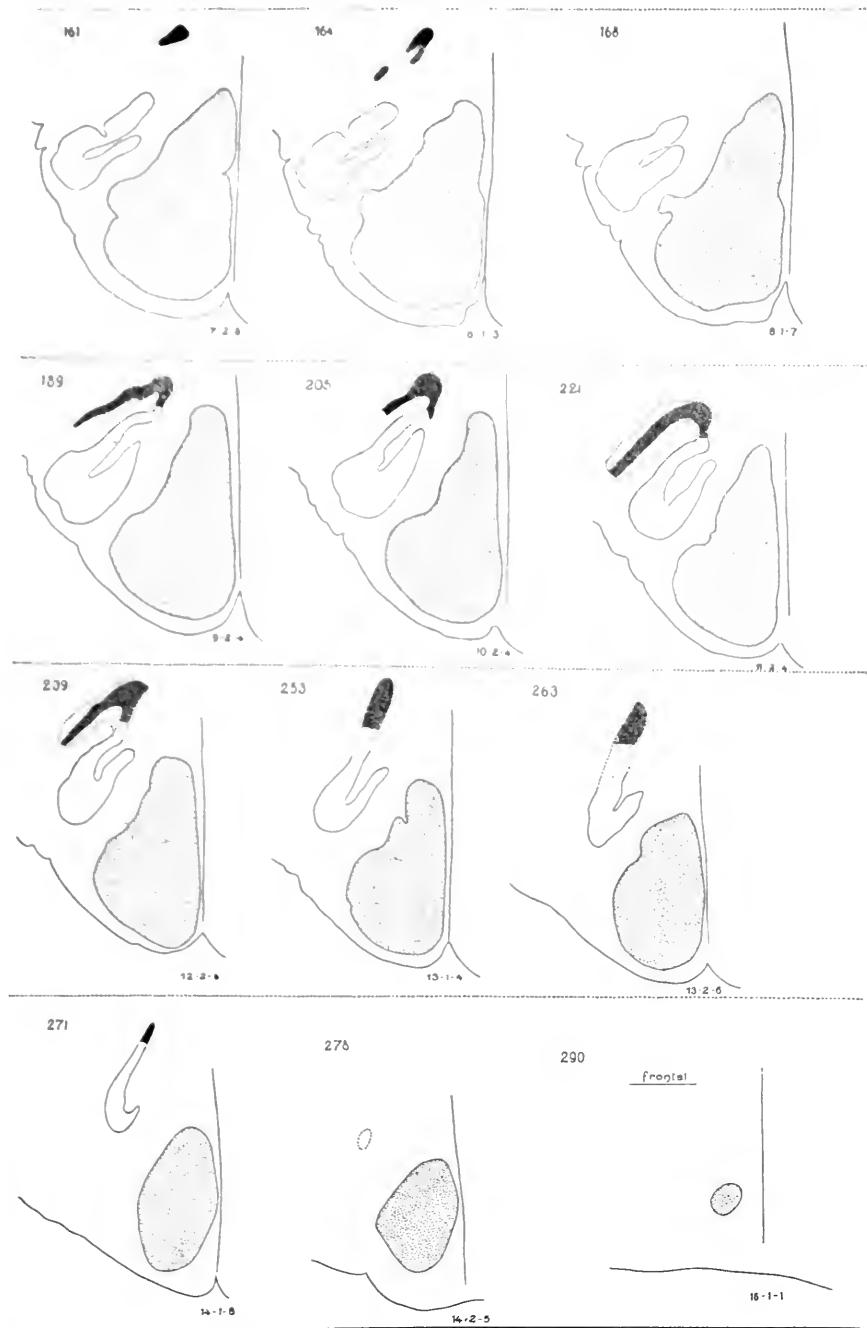


Table 40bis.

Like in *Phocaena*, the dorsal cap is present, though less distinct (Table 40, s. 36 etc.). Together with the rest of the caudal part (of the medial olive), it lies dorsally on the large frontal part and gradually disappears (Table 40, s. 64—139).

At the caudal appearance of the principal olive, the cap shows an outgrowth, which is directed towards that olive-part (Table 40, s. 96—139). As it resembles the same condition in *Elephas* and *Phocaena* very much, it confirms the correctness of my interpretation there (*vide infra*).

The frontal part of the medial olive appears ventrally of the caudal one, free from other olive-parts, as it is quite surrounded by a thick fleece of fibres.

Developing enormously, it produces a protrusion on the surface of the bulb; it is wedge-shaped, with a lateral shallow, caused by a sudden widening of its base (Table 40, s. 127, 137, 139). At the caudal appearance of the principal olive, it becomes narrower (Table 40, s. 153 etc.); more frontally it decreases in all directions (Table 40, s. 221), in most frontal sections even very rapidly.

The dorsal olive is poorly developed in *Tursiops*.

Only in a few sections (Table 40, s. 71—92), it can be decidedly ascertained; caudally it has the form of a rather thick plate (s. 92—139), more frontally it seems to be only an about round cell-accumulation, lying very dorsally of the rest of the olive (s. 153—164). Still more frontally, its presence cannot be absolutely ascertained. Yet I do not believe this dorsal olive to be an exception.

The V-shape is visible also here; more-over, it resembles the same part in *Phocaena* very much, though it is still more indistinct; like in *Phocaena* it bends into the dorsal lamella of the principal olive and most frontally seems to form the dorsal top of this lamella (Table 40, s. 253—271).

The ventro-lateral (principal) olive appears caudally (Table 40, s. 127), free from the other parts, quite near the border of the bulb.

Most caudally the dorsal lamella is best developed, a little higher the medial lamella is about equally long. In the most frontal sections, however, it becomes much shorter, though the proportion is probably exaggerated in favour of the dorsal lamella by its prolongation with the dorsal olive (Table 40, s. 253—271).

The principal olive disappears exactly below the frontal top of the medial one.

Ungulata.

Sus scrofa L. (domesticus). — Waxreconstruction: Figs. 78, 79, 80,
Table 41.

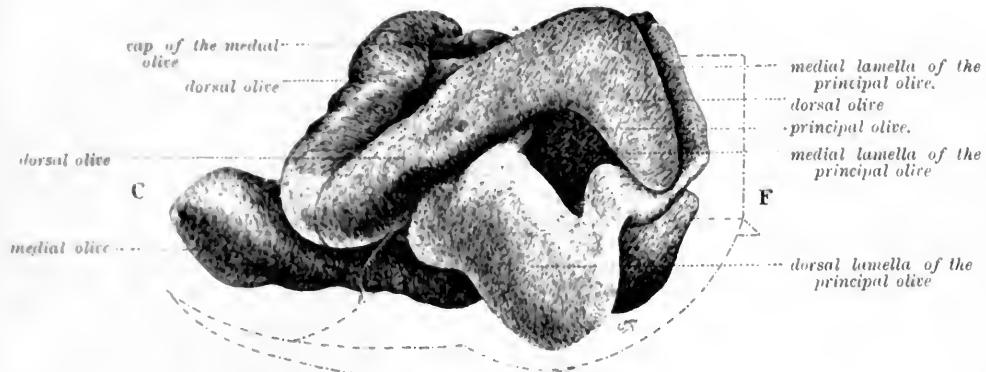


Fig. 78.

Inferior olive of *Sus scrofa L. (domesticus)* $\pm 48 \times$ (frontal and lateral view).

The medial olive, and especially its ventral component is large; this part extends far laterally, (Table 41, s. 1—85); its ventral groove is very distinct (indicated by a in the table); in higher sections this groove shifts a little medially and then becomes connected with the dorsal curvature, which separates the medial component from the ventral one (Table 41, s. 93).

These grooves give a sinuous appearance to the medial olive (Table 41,

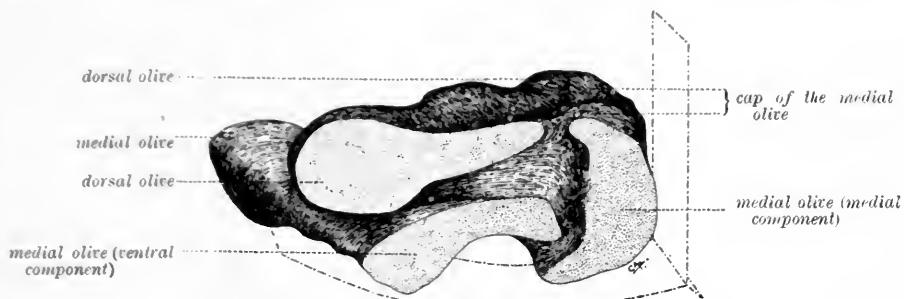


Fig. 79.

Inferior olive of *Sus scrofa L. (domesticus)*; caudal part in frontal view.

s. 57—85); when they communicate, the medial olive is divided into two separate parts (Table 41, s. 93—105). The medial component, which shows a distinct dorsal cap (Table 41, s. 81—93) disappears at the caudal end of the principal olive, which at that level is closely connected with the cap (Table 41, s. 93—105, see also the model fig. 80). More frontally the

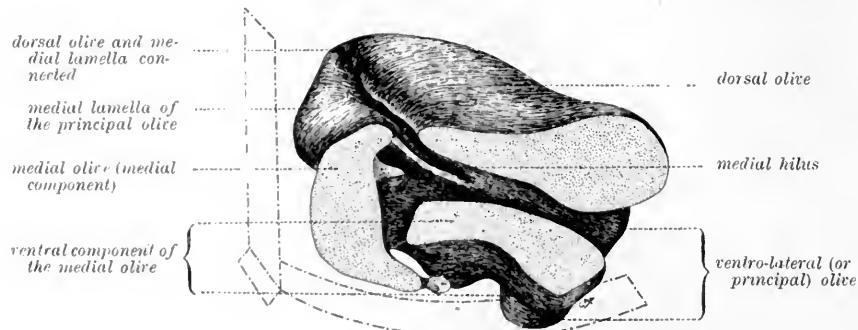


Fig. 80.

Inferior olive of *Sus scrofa L. (domesticus)*; frontal part in caudal view.

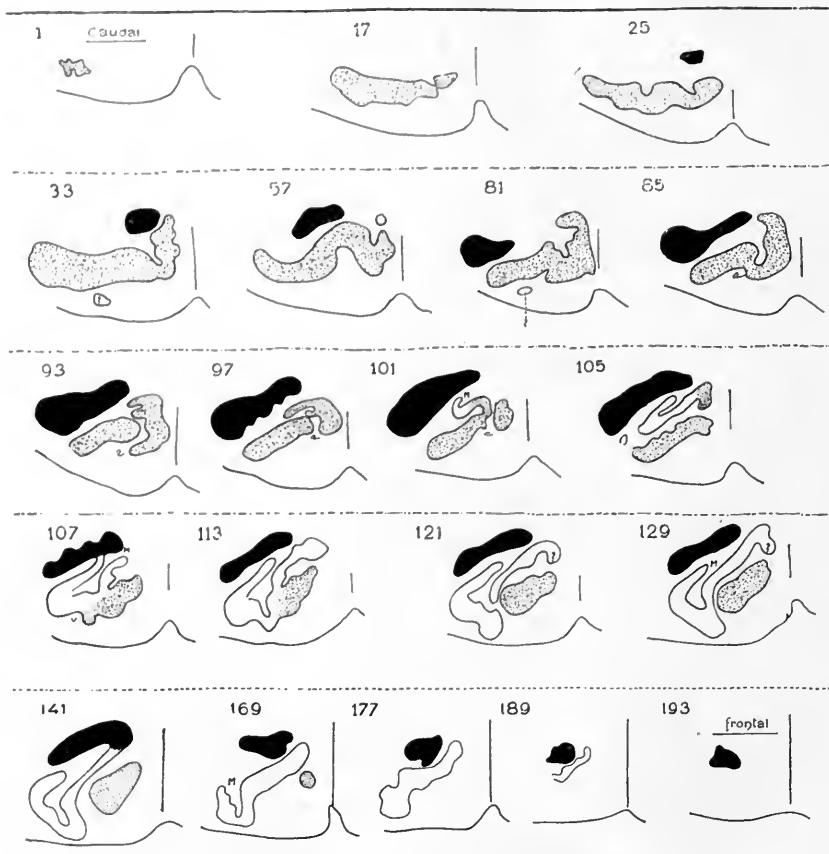


Table 41.

Abbreviated order of sections through the inferior olive of *Sus scrofa L. (domesticus)*.
Magnified $\pm 6 \times$.

medial part having disappeared, the ventral component¹⁾ lies in a plane which forms an angle of about 45° with the raphe (Table 41, s. 101—141).

The dorsal olive extends a little less far caudally than the medial one, it shifts laterally, (Table 41, s. 25—81) and retakes its medial position at about the first appearance of the principal olive (forming a very distinct V-figure in the model). It is rather large, especially over its frontal half, during the presence of:

The ventro-lateral olive.

This part begins at about the middle of the olive-length as a ventro-lateral outgrowth of the dorsal cap of the medial olive (Table 41, s. 97 a. s. o., see also the model).

It soon shows two lamellae, the dorsal one of which is free and the medial one connected with the above-mentioned cap. Speaking generally, the dorsal lamella remains free, whereas the medial one is connected with the medial olive in several sections (Table 41, s. 101—113).

More frontally, the medial lamella becomes longer, its dorsal top bends ventrally (Table 41, s. 113—129). While the dorsal lamella becomes shorter and disappears (Table 41, s. 169—177), the medial one remains, almost until the frontal end, together with the dorsal olive. The latter, however, reaches most frontally; as the figures show, the dorsal and the medial olives are well-developed in all dimensions.

Capra hircus L. — Table 42.

The olive in Capra resembles that in Sus very much.

The medial olive is still more sinuous, the ventral and the dorsal grooves being deeper.

The dorsal cap is distinctly visible. Also in Capra, the ventral component remains in frontal sections, after the medial one has disappeared (this is contrary to the rule with Mammals).

The dorsal olive is well-developed, it begins more frontally than in Sus and has a very pronounced V-shape.

For the rest, it is quite analogous with the same part in Sus (see Table 42).

The ventro-lateral (or principal) olive also resembles that of Sus, only is its caudal end not connected with the medial olive. A little more frontally, however, this is the case with the medial lamella (cf. s. 150—288, Table 42 with s. 101—189, Table 41)²⁾.

Note 1: This way of putting things is not quite accurate. The ventral groove deepens and finally divides the medial olive into two parts, of which the lateral one remains; so the part, situated medially of the ventral groove, disappears together with the medial component; the same is seen with other Ungulates and with Sirenia.

Note 2: I cannot give an interpretation of the small cellbody, situated between the dorsal and the principal olive (Table 42, s. 165—245).

Equus caballus L. — Table 43.

The olive in *Equus* resembles that of *Sus* and *Capra* very much, as well in its principal lines, as in many details.

The medial olive, especially its ventral component, is strongly developed and still more so is the dorsal one.

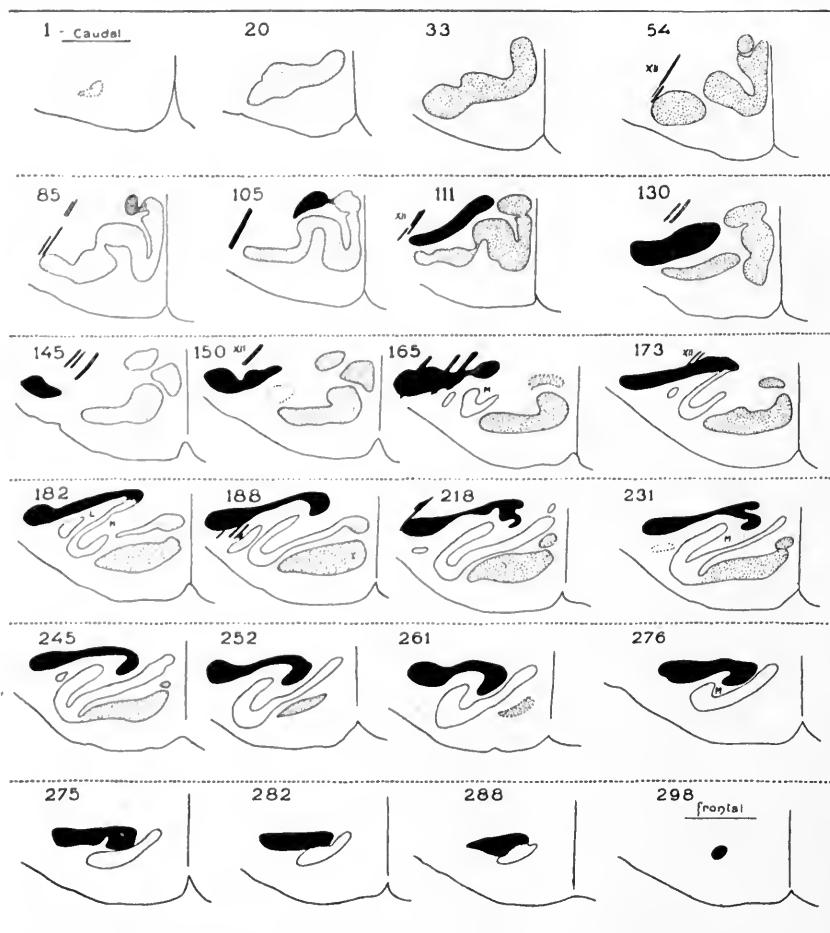


Table 42.

Abbreviated order of sections through the inferior olive of *Capra hircus L.*
Magnified $\pm 6 \times$.

The medial olive is sinuous; like its predecessors, it shows a tendency to divide itself into a free ventral and a medial part¹⁾; its cap is connected with the caudal end of the principal olive by a well-

Note 1: See Note 1 of page 93.

developed, ventro-laterally directed outgrowth (Table 43, s. 154—177).

In *Equus* also, only the ventral component remains over the frontal half; it is then placed in the same plane as the other olive-parts.

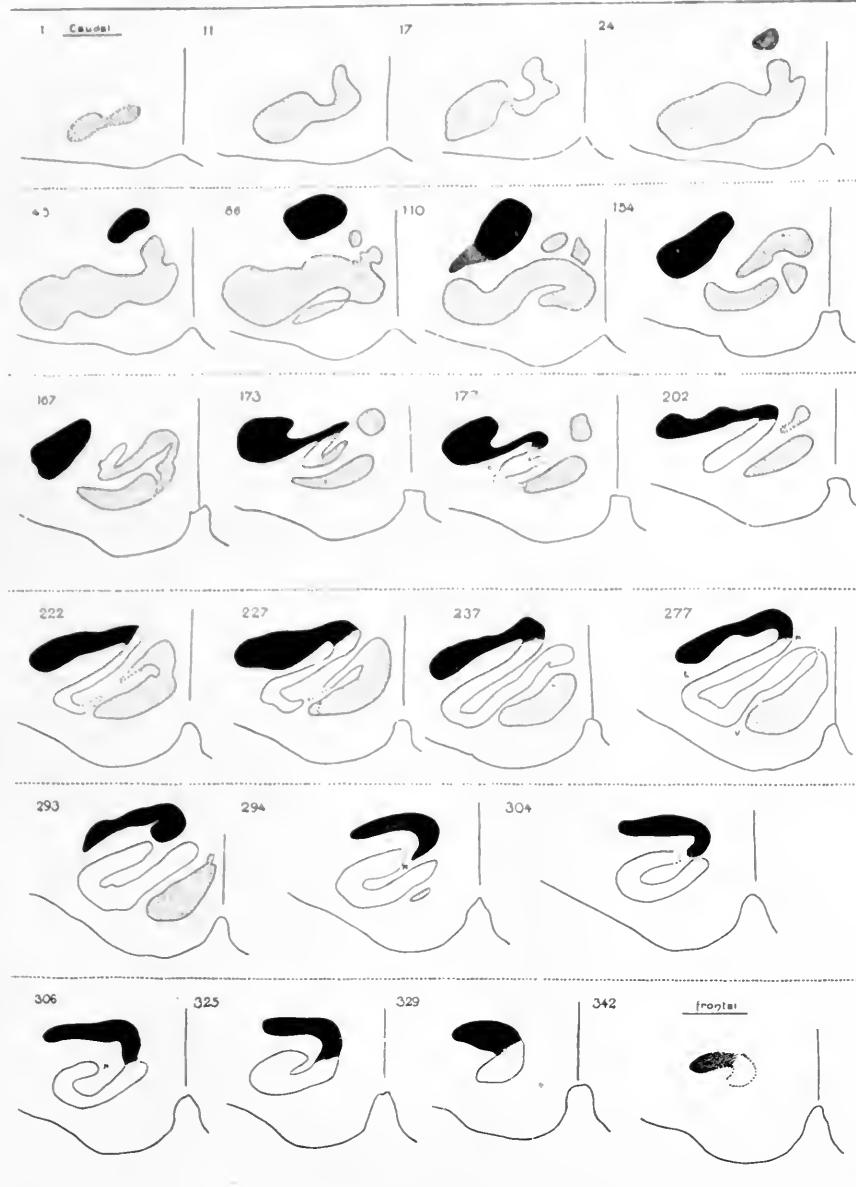


Table 43.

Abbreviated order of sections through the inferior olive of *Equus caballus* L.
Magnified $\pm 2.5 \times$.

The dorsal olive begins on the same level as in Capra, and has also the same form.

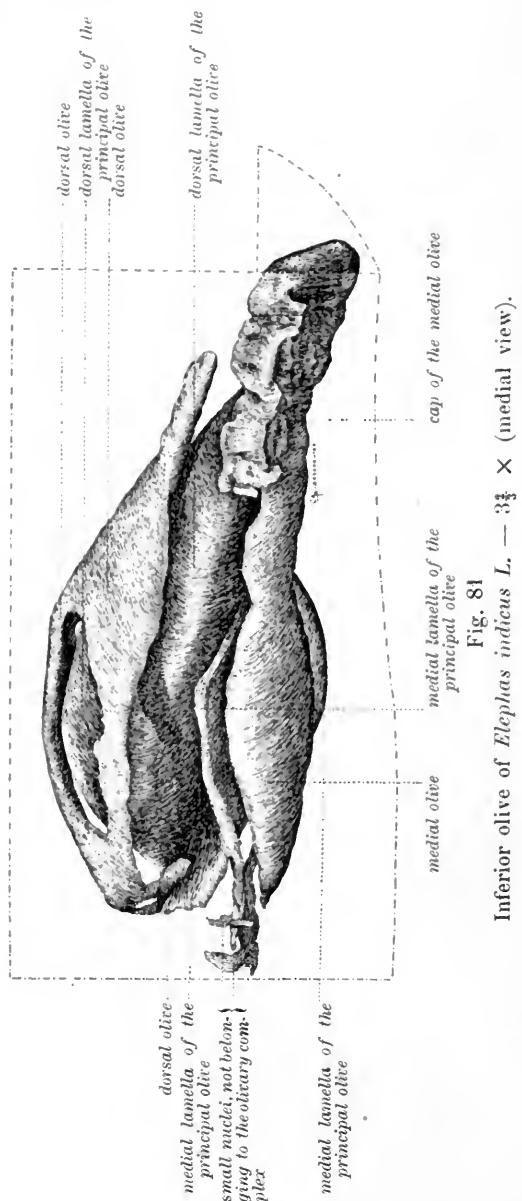


Fig. 81

Inferior olive of *Elephas indicus* L. — 3½ X (medial view).

At the caudal appearance of the principal olive, it again turns medially and shows in these sections a dorsal thickening, which resembles that in *Erinaceus* very much (Table 43, s. 173—177).

It is connected with the dorsal lamella of the ventro-lateral olive over a far greater distance than in the other two Ungulates. Over the frontal half, however, when the dorsal lamella becomes shorter, the dorsal olive takes the same position as described in the two other Ungulates (Table 43, s. 293—342).

The ventro-lateral or principal olive, beginning caudally at about the middle of the olfactory complex, first shows only a dorsal lamella. The ventral lamella appears higher than in *Sus* and *Capra* (Table 43, s. 222) and is closely connected with the cap of the medial olive.

The medial, lateral and ventral¹⁾ hiluses are very well visible. (Table 43, s. 277).

More frontally, the dorsal lamella is the first to get shorter, the ventral one seems to be present at the same time with the dorsal olive until the frontal end.

Proboscidea.

Elephas indicus L. — Wax-reconstruction: Fig. 81, Tables 44 and 45.

Note 1: By ventral hilus is meant the one between the medial and the principal olive, whereas the lateral hilus separates the latter olive-part from the dorsal one.

The medial olive, as usual reaching most caudally, shows a distinct ventral groove (Table 44, s. 91); a division into a ventral and a medial component is hardly possible; at the caudal appearance of the principal olive a dorsal cap is visible, with an outgrowth which is directed ventro-laterally.

This is the case with many Mammals, as has already been described for *Lepus*, *Arctomys*, *Canis*, *Sus* and *Equus*.

In *Elephas*, however, these sections cause some difficulties. I therefore made a separate table of an abbreviated order of sections from

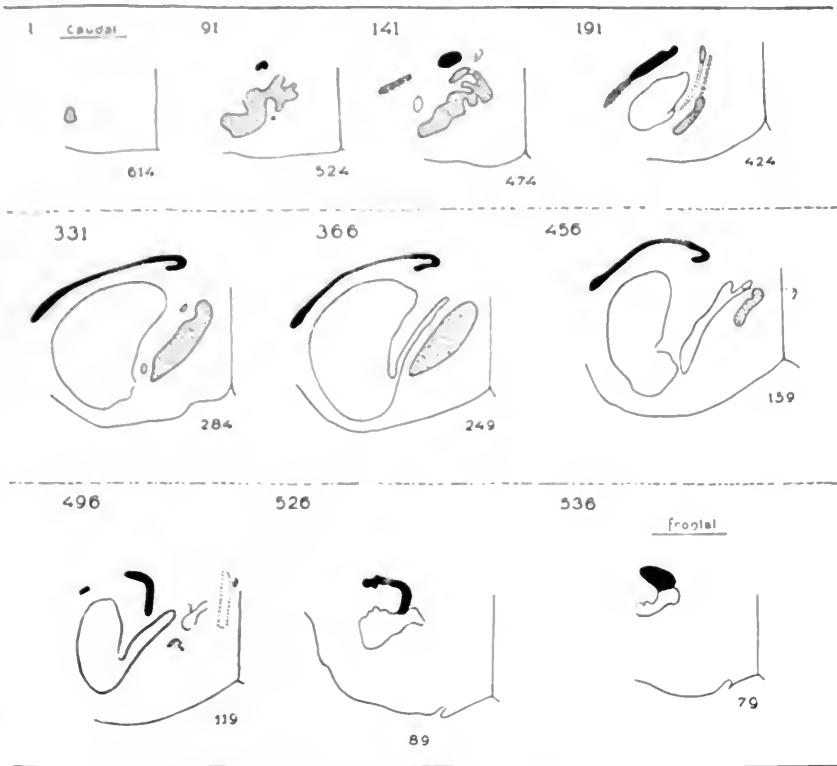


Table 44.

Abbreviated order of sections through the inferior olive of *Elephas indicus L.*

Size of the section = 250μ . Magnified $\pm 1.5 \times$.

s. 116—201, showing the various forms of the medial olive on that level.

Only that part of the medial olive was modelled, which was distinctly visible.

Dorsally on this part lies a kind of cap, very indistinctly outlined, of which only two small pieces are a little more distinct (α and β , Table 45, s. 116).

At about the caudal appearance of the principal olive, these pieces

(α and β), are united, and form one small strand of grey substance (Table 45, s. 151), which in the following sections moves in a ventro-lateral direction, lying alongside the medial olive and becoming connected with it. Only a comparison with many other mammalian olives can give the interpretation here.

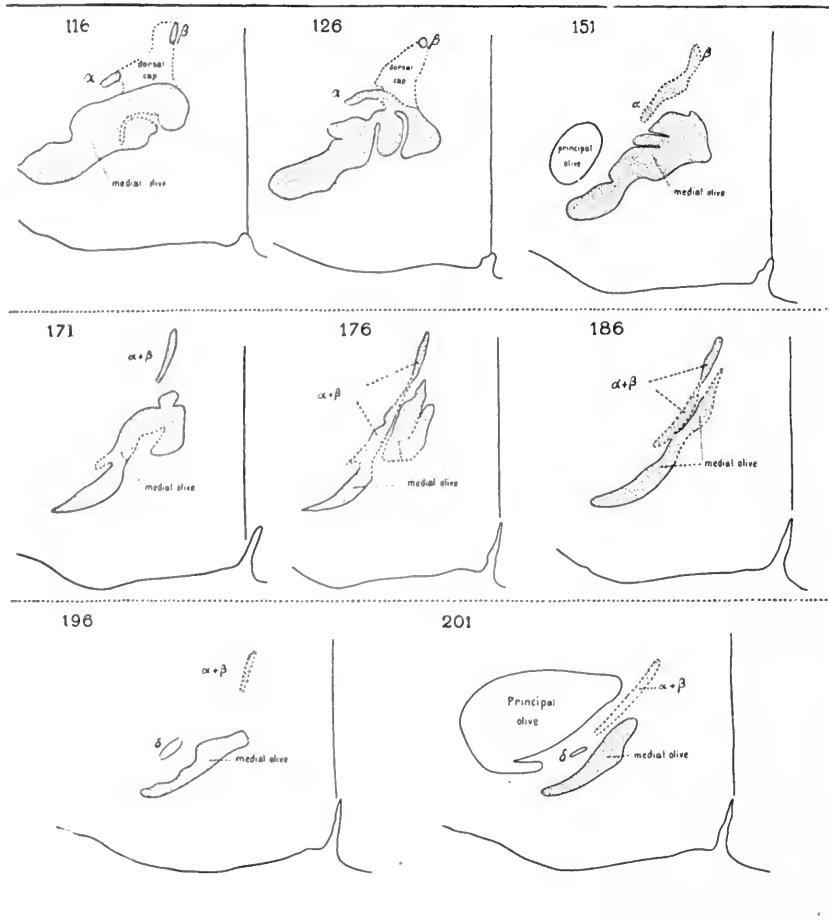


Table 45.

Abbreviated order of sections through a part of the medial olive in
Elephas indicus L.

Magnified 3.5 \times .

Still more frontally, the outgrowth (α and β) gets free once more and disappears when the principal olive becomes fully developed.

What makes matters still more intricate, is that on this level also a small cell-accumulation appears, which gives the impression of being

a prolongation of the medial lamella and also disappears in more frontal sections (Table 45, δ).

Of the medial olive, the ventral part remains; more frontally, it gradually increases (Table 44, s. 331—366), to diminish once more on a much more frontal level.

So in Table 45, I interpreted the various parts thus: α and β correspond to the usual ventro-lateral outgrowth of the dorsal cap, which in *Elephas* is very indistinct; δ probably corresponds to the first development of the medial lamella, which in other Mammals is found on that level, but which in *Elephas* has shifted frontally by the enormous development of the dorsal lamella.

In caudal sections, *the dorsal olive* has a quite dorsal position and is about round; more frontally it extends laterally, so that it lies like a large thin plate over the enormous dorsal lamella of the principal olive; the medial and the lateral part of this plate are distinct; the connecting part, which lies over the dorsal top of the above-mentioned dorsal lamella, is very thin and often difficult to see. Only the distinct parts were modelled, so that in fig. 81 the gap must be thought filled up by a very thin layer of cells. In Table 45, the thin indistinct parts are darkly dotted. Already in the caudal half, the medial part of the dorsal olive bends like a hook to ventrally, without becoming connected with the principal olive, however, as is the case with other Mammals.

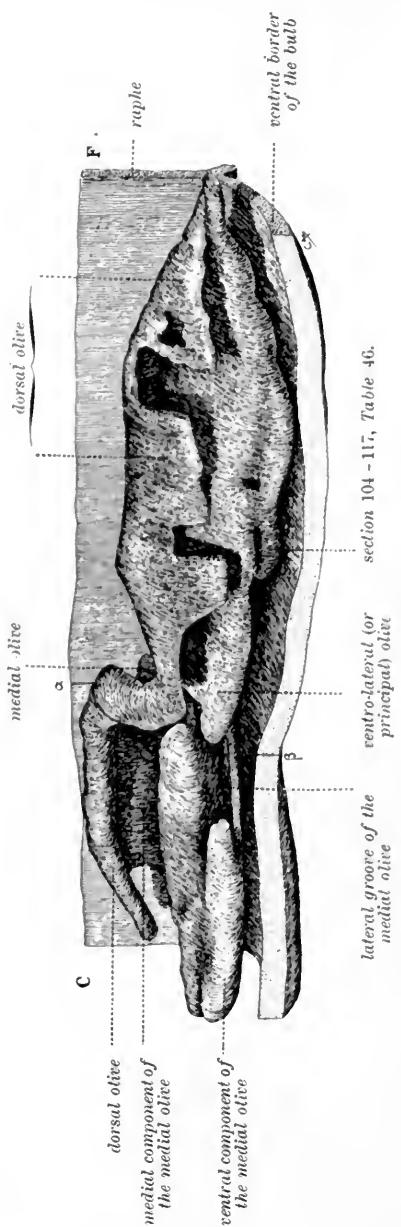
In *Elephas*, the dorsal lamella of the principal olive has grown enormously, has become free from all other parts and is surrounded by a thick fleece of fibres; perhaps this is the reason why the dorsal olive is nowhere connected with it.

Quite frontally, the dorsal olive blocks up the medial hilus and gets connected with the medial lamella (Table 44, s. 496—526).

The ventro-lateral or principal olive is also free from the other olive-parts at its caudal end. Because of the huge development of the dorsal lamella, it occupies about 75 % of the length of the olive. This dorsal lamella soon becomes very large in all dimensions, whereas the medial one remains undeveloped until a much more frontal level, when it extends dorsally, but then also, it remains a very thin plate, as contrasted with the dorsal lamella. The latter, however, is the first to disappear; the ventral lamella shows a medial side-branch (γ), which gets free from the lamella and becomes connected with a small cell-accumulation (ζ), situated more ventrally and with an indistinct cell-mass along the raphe (θ). Part γ , which bends ventrally, probably corresponds to the dorsal top of the medial lamella in other Mammals, its cell-type is indeed very like that of the medial lamella.

I do not consider the parts ζ and ο to belong to the olfactory complex.

Most frontally, the medial lamella gets connected with the dorsal olive; together they form the frontal top of the whole complex.



Inferior olive of *Halicore dugong* Erxleb. — 8 × (lateral view)
Fig. 82.

Sirenia.

Halicore dugong Erxleb. —
Waxreconstruction: Figs. 82, 83,
84; Table 46.

Two deep grooves, a medial and a lateral one, make the *medial olive* very sinuous (see for the lateral groove fig. 82, for the medial one fig. 83). This sinuous ventral component bends into a straight, thin medial one, forming an acute angle. The medial component shows the usual dorsal cap. Though the ventral part of the *medial olive* is more than usually winding, there is no real difference between it and the corresponding parts in *Sus* and *Capra* (see fig. 85; in *Macropus* one sees that the groove which in most Mammals opens ventrally, can also open more medially; the *medial olive* in *Halicore* has exactly the same form as that in *Capra*. This resemblance between *Halicore* and the Ungulates is interesting, since we know that also in other points Sirenia are, of all Mammals, next to the Ungulates).

In both groups, Sirenia and Ungulata, the ventral and the medial component become sepa-

rated¹⁾ (Table 46, s. 61, fig. 83, 84); of these two the ventral one remains, occupying most frontally a medial position.

Note 1: See Note 1, page 93.

In caudal sections *the dorsal olive* has a round form and is connected with the cap of the medial olive, from which it gets free at the caudal appearance of the ventro-lateral olive. It then takes a more lateral position (Table 46, s. 67—78) and more frontally covers the dorsal lamella

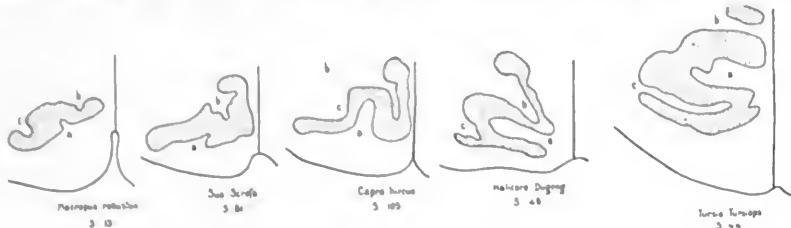


Fig. 85.
The grooves of the medial olive. — 5.5 X.

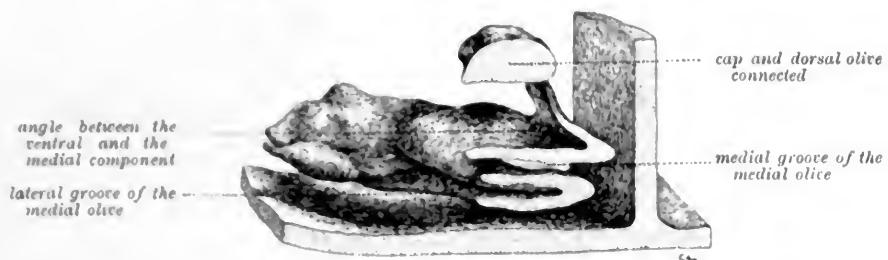


Fig. 83.
Inferior olive of *Halicore dugong* Erxleb.; caudal part in frontal view.

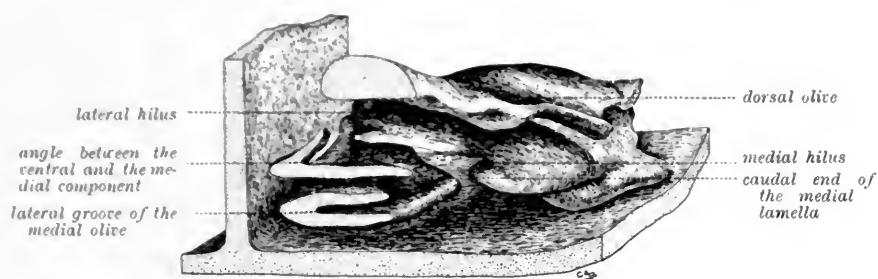


Fig. 84.
Inferior olive of *Halicore dugong* Erxleb.; frontal part in caudal view.

of the principal olive like an extensive plate. The middle-part of this plate is very indistinct, containing only very few cells; it is indicated in the table by dots and forms a gap in the model. In some sections (Table 46, s. 100—104) the dorsal olive is connected with the dorsal lamella of the principal olive, more frontally it is hooked and blocks up the medial hilus (Table 46, s. 156—182); finally it becomes connected

with the medial lamella. From this, it appears that also the dorsal olive is quite analogous with that in Ungulates.

The *ventro-lateral olive* (principal olive) occupies about 62.5 % of the total length of the olive; the dorsal lamella reaches most caudally;

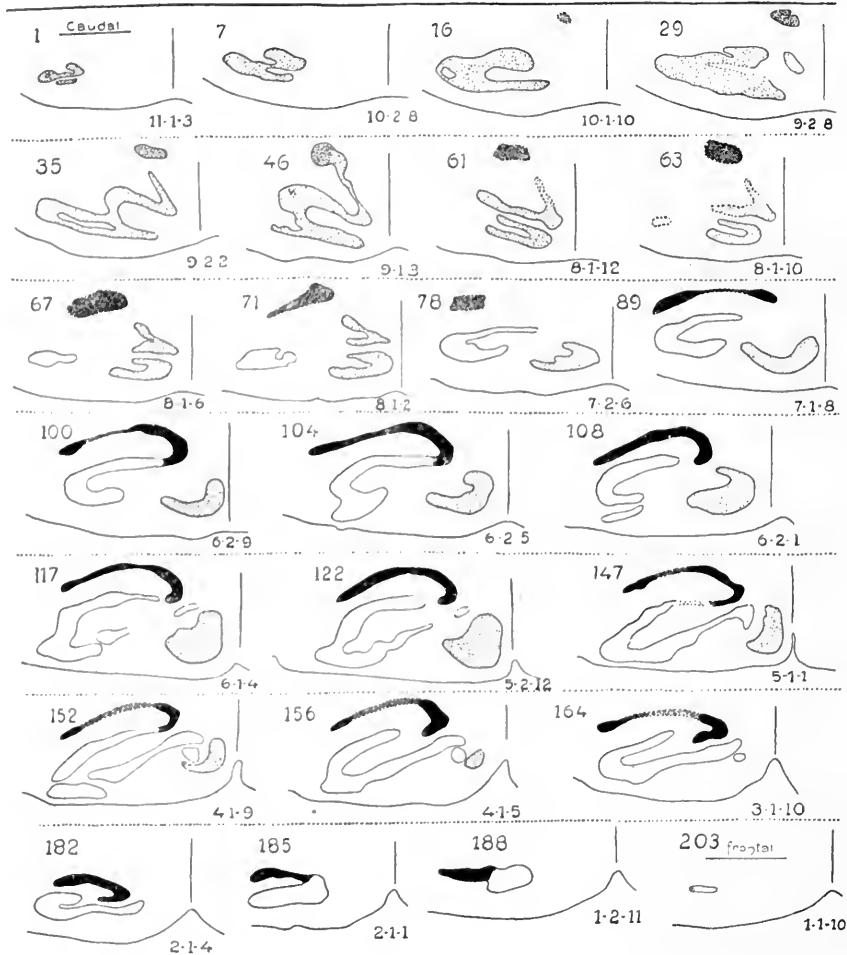


Table 46.

Abbreviated order of sections through the inferior olive of *Halicore dugong* Erxleb.
Size of the section = 60 μ Magnified $\pm 6 \times$.

more frontally the medial one is also present, it becomes, however, only well-developed on a much more frontal level.

While the medial lamella becomes longer, the dorsal one gets shorter and is the first to disappear. The dorsal top of the medial lamella

bends ventrally and becomes independent (the same was seen in *Sus* and *Capra*). Of the two lamellae, the medial one reaches most frontally (as mentioned above), as was also the case with Ungulates.

Manatus latirostris Harlan. -- Waxreconstruction: fig. 86, Table 47.

The material was rather old, so the stain is not very good, besides this, only few sections were preserved, so that each section represents 250 μ . On account of this, it seems probable that section 1 is not quite the most caudal (see also fig. 86, where the unfinished model is drawn).

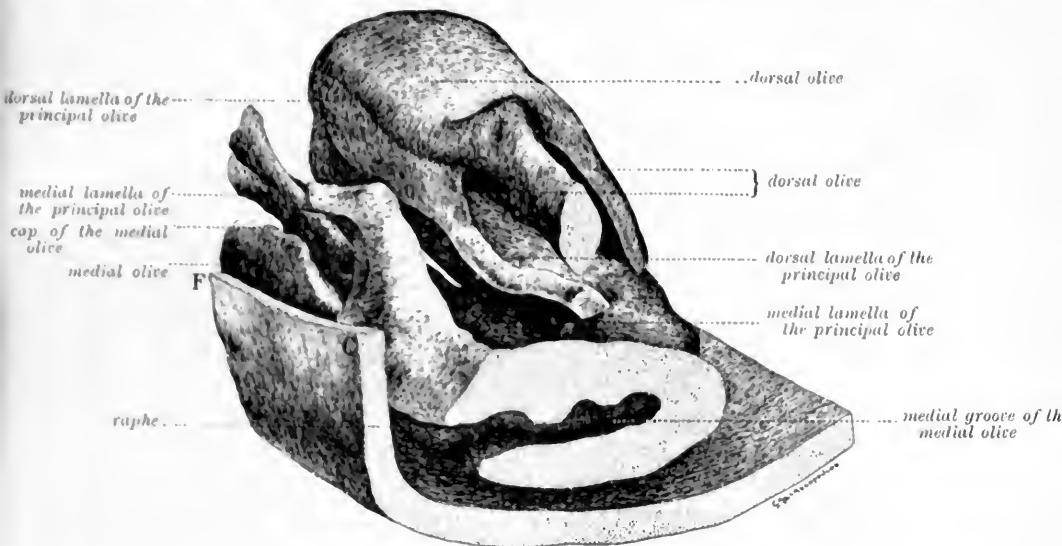


Fig. 86.

Inferior olive of *Manatus latirostris Harlan.* $\pm 18 \times$ (caudal and medial view).

In the medial olive we see a distinct medial groove, corresponding to the ventral groove in other Mammals. A dorsal cap is visible, which disappears at the caudal end of the principal olive.

Like in Halicore, in frontal sections only the ventral component is present, which is gradually confined to its most medial part.

Laterally of the medial olive, as long as the olive-complex is present, we find a small nucleus, which I did not consider to belong to the olfactory complex (indicated in Table 47 by single cross-hatching).

The dorsal olive does not show the usual V-shape; in caudal sections, however, it has, like in other Mammals, a dorsal position and takes the plate-form at the caudal appearance of the principal olive; as has been described for Halicore, its medial part is most distinct. The dorsal olive remains until the frontal end of the olive.

The principal olive is well-developed, both lamellae are distinct, and separated by a wide medial hilus. The lateral hilus is also wider than usual, as can be seen in the table.

The ventro-lateral olive occupies 78 % of the total olive complex

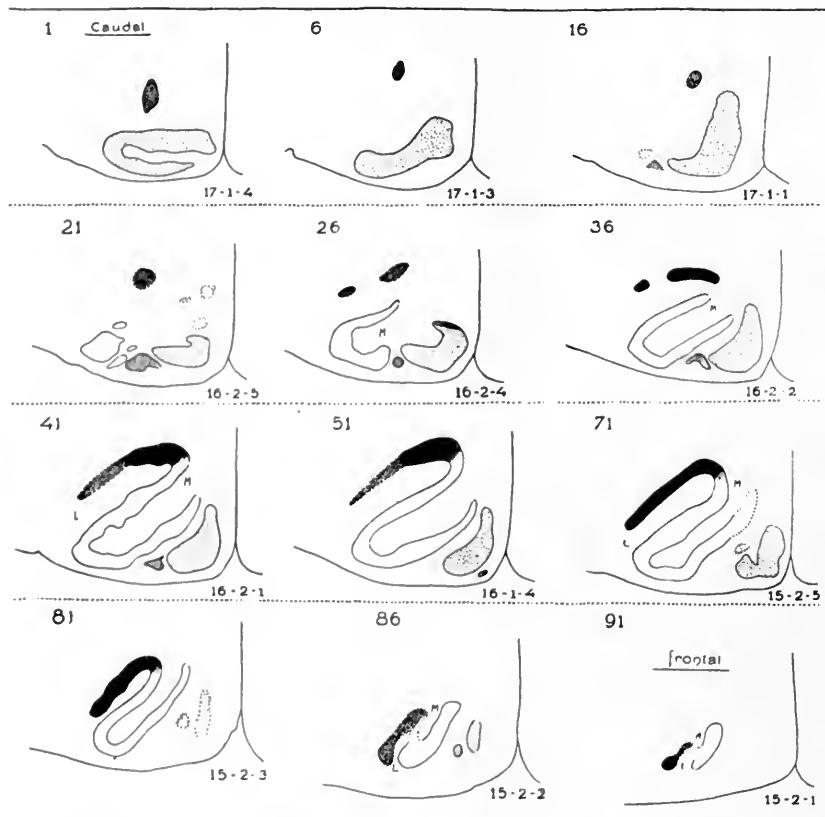


Table 47.

Abbreviated order of sections through the inferior olive of *Manatus latirostris* Harlan.

Size of the section = 250 μ .

Magnified $\pm 6 \times$.

(as drawn in the table; this is, however, probably exaggerated because of the abrupt caudal end of the medial olive).

Both lamellae are of about the same length; only on a very frontal level the medial lamella is a little longer than the dorsal one.

Primates.

Lemur catta L. — Table 48.

The medial olive reaches most caudally; a ventral groove is visible (Table 48, s. 33—58).

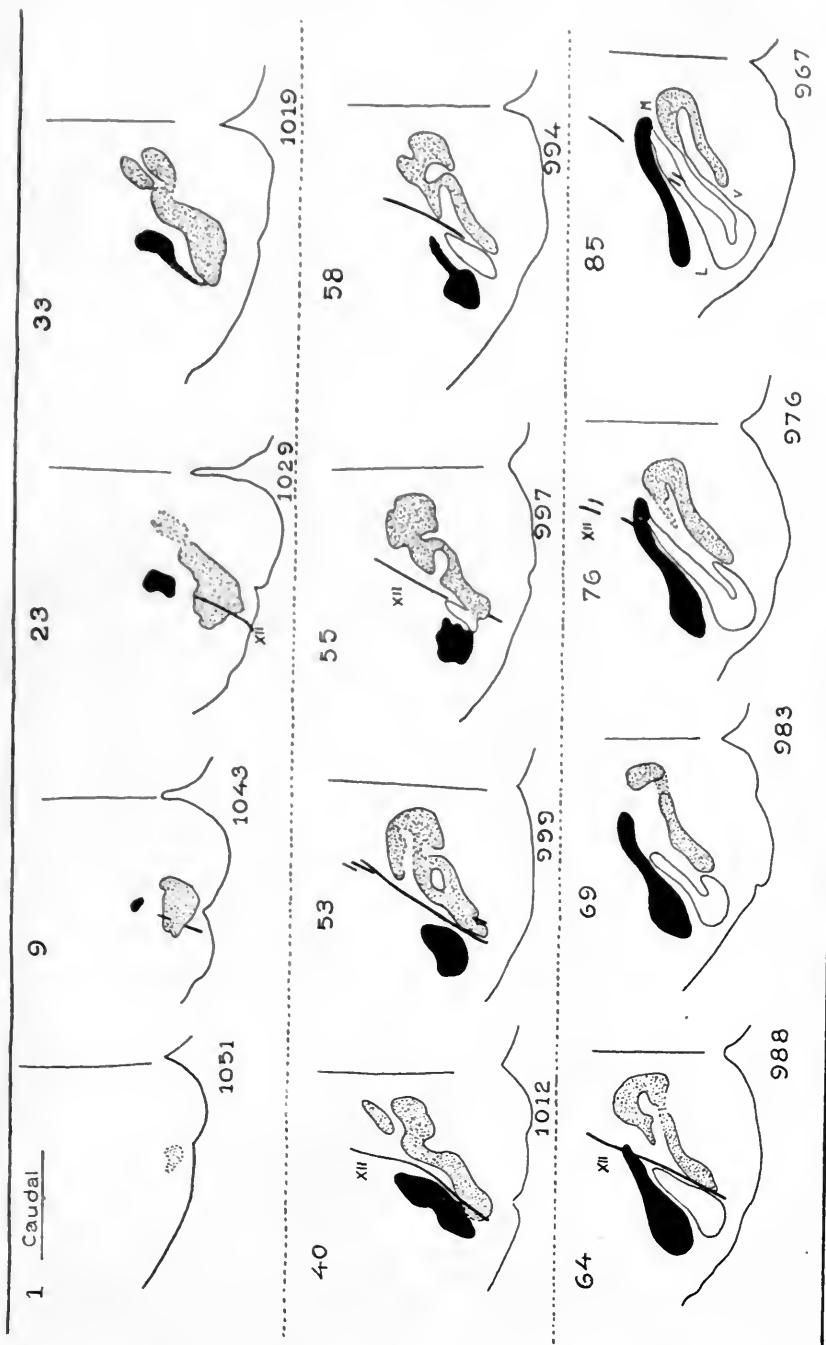


Table 48.
Abbreviated order of sections through the inferior olive of *Lemur catta L.*.
Size of the section = 70μ . Magnified $\pm 10 \times$.

It is possible to make a division into a ventral and a medial component; the medial one has a dorsal cap with a ventro-lateral outgrowth at the caudal appearance of the principal olive.

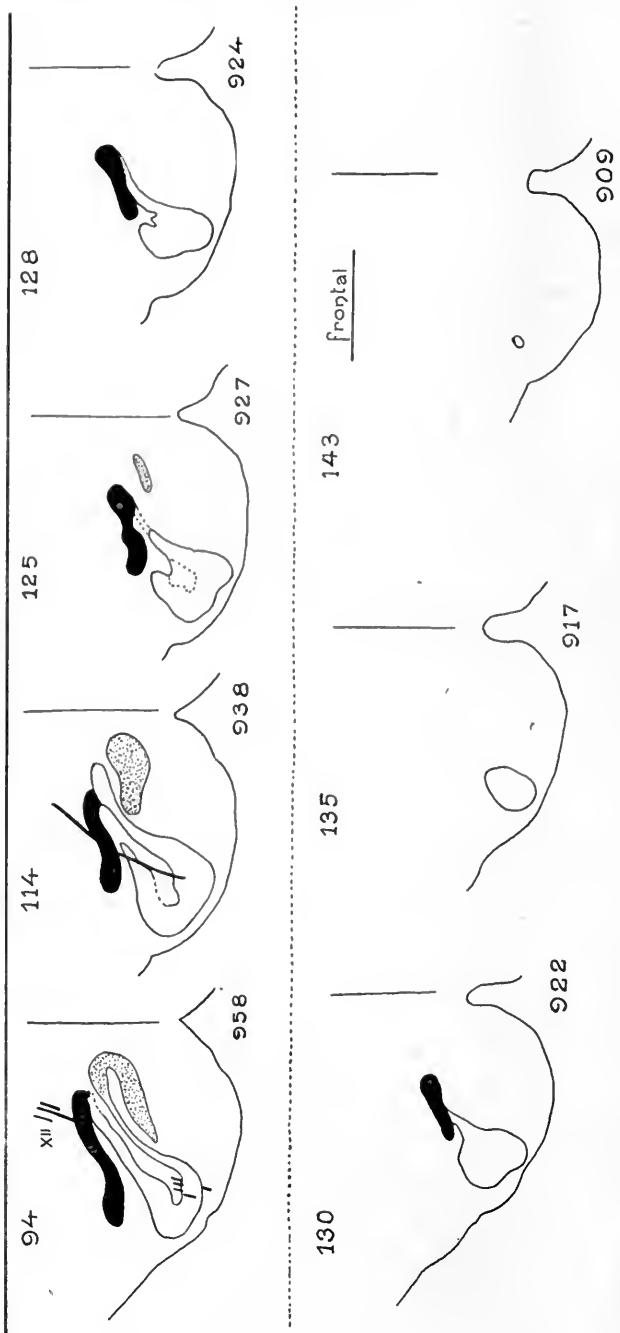


Table 48bis.

Frontally, the cap disappears, the ventral part remains and then occupies a more medial position.

The dorsal olive has the typical V-shape, the ascending line of which is a long extensive plate, while the two lines meet at the level of the first caudal appearance of the principal olive (Table 48, s. 55—58). Caudally, the dorsal olive is connected with the dorsal lamella of the principal olive (Table 48, s. 76—94), finally with the medial one.

It disappears a little below the frontal top of the total olfactory complex.

The ventro-lateral (or principal) olive occupies 62 % of the length of the total olfactory complex.

As usual, the dorsal lamella is caudally developed best, whereas more frontally, also the ventral lamella is developed and even better so.

Only a few sections (Table 48, s. 85—94) show the „Vierblättertypus”; most frontally, the two lamellae melt together, while the frontal top is stretched out rather thinly (Table 48, s. 135—143).

Oedipomidas oedipus. — Waxreconstruction: Fig. 87, Table 49.

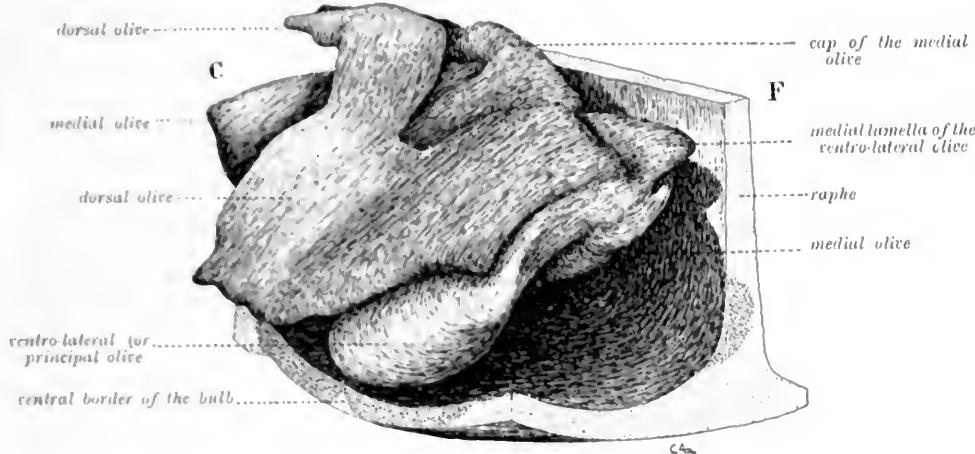


Fig. 87.
Inferior olive of *Oedipomidas oedipus*. — 27 X (fronto-lateral view).

The *medial* and the *dorsal olive* are rather well-developed. The ventral groove is visible (Table 49, s. 17—24) and so is the dorsal cap, with its ventro-lateral outgrowth at the caudal end of the principal olive. Like in most Mammals, the ventral and the medial component are not situated perpendicularly on each other (as is f. i. the case with Ungulates), but form a nucleus, lying in the well-known slanting plane, which makes an angle of 45° with the raphe.

In most frontal sections, the medial part of this nucleus remains.

The *dorsal olive* shows the common V-shape (fig. 87) successively having a dorsal, a lateral and again a dorsal position; its frontal part extends like a plate along the dorsal lamella of the principal olive. Most frontally it bends like a hook round the top of the dorsal lamella, blocks up the medial hilus and gets connected with the medial lamella (Table 49, s. 43 etc.).

The *principal olive* is only present over the smaller frontal half of the olfactory complex (45%). Also by form, this olive-part is rather pri-

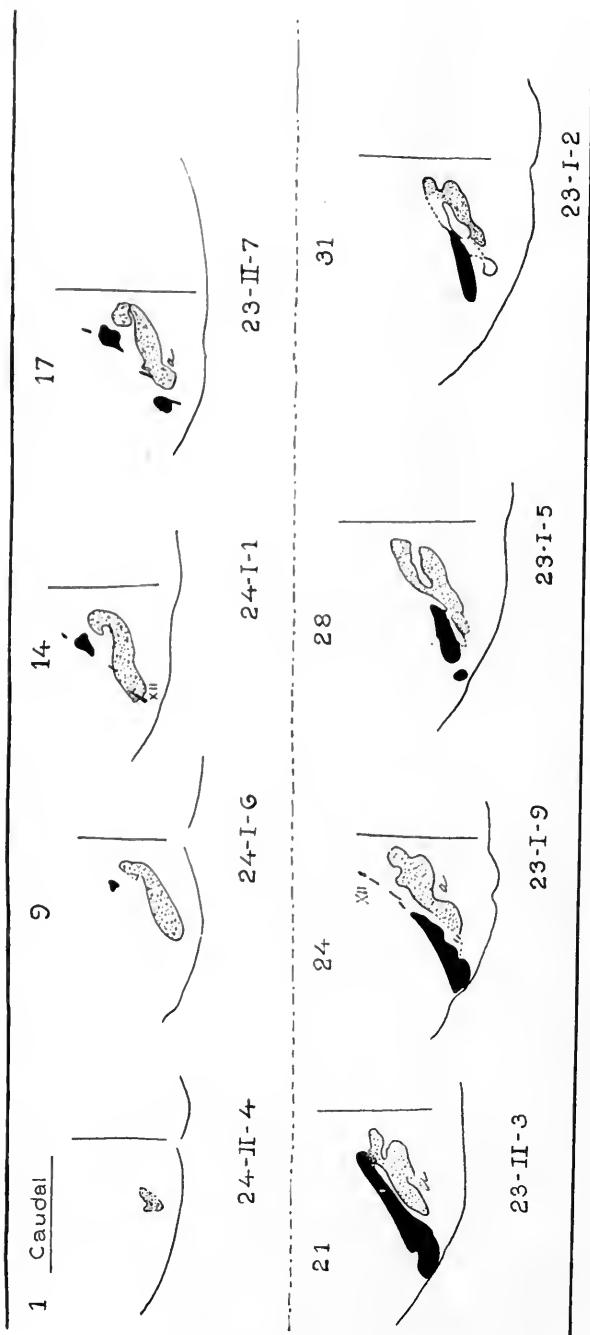


Table 49.
Abbreviated order of sections through the inferior olive of *Oedipomidas oedipus*.
Size of section = 60 μ . Magnified + 10 X.

primitive, for only in a few sections the two lamellae with the medial hilus are well-developed (Table 49, s. 38—43).

The dorsal lamella is largest in caudal sections, the ventral one on a frontal level; they melt together on the frontal top.

Hapale pennicillatus E. Geoff.
Table 50.

The medial olive, the most caudal olive-part, is well-developed. It is present until almost the frontal end of the total complex.

Over its caudal half a division into the ventral and the medial component is possible (Table 50, s. 13—77).

The ventral groove is only slightly visible (Table 50, s. 25—57); the dorsal cap is also present, it shows the usual ventro-lateral outgrowth, which is connected with the cau-

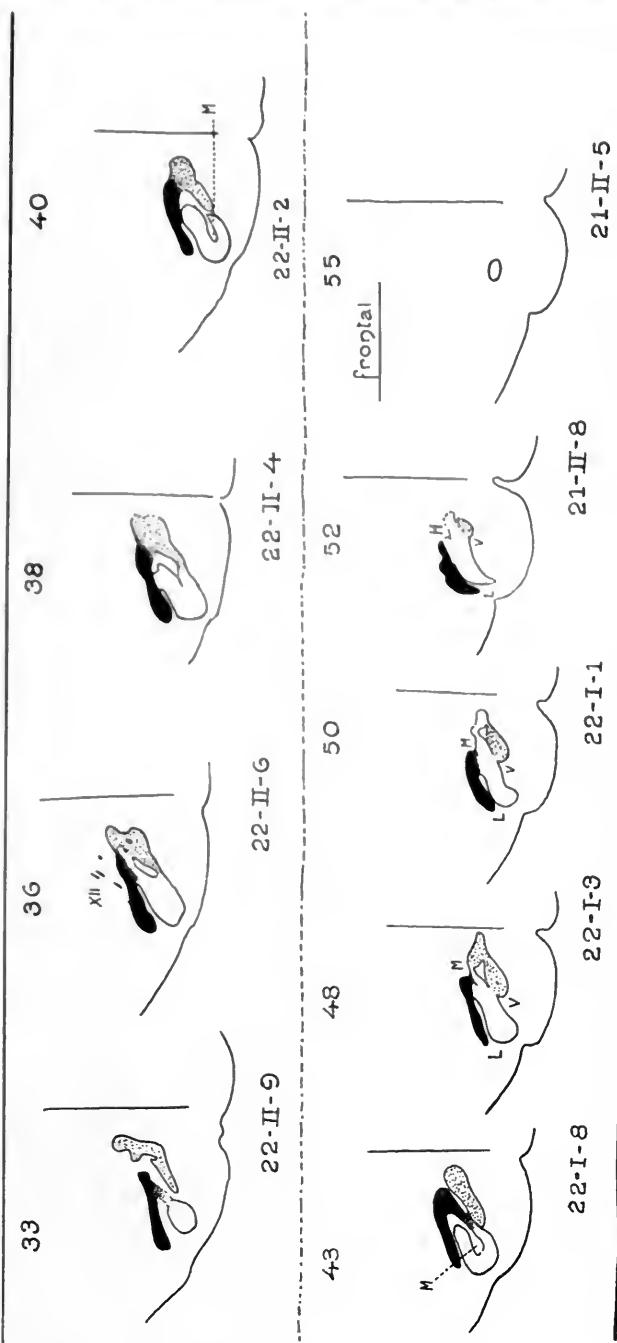


Table 49bis.

dal end of the principal olive. When the ventro-lateral olive becomes better developed, the cap disappears; the medial olive extends rather far laterally, also in more frontal sections (Table 50, s. 129—169), only at the end it takes a more medial position.

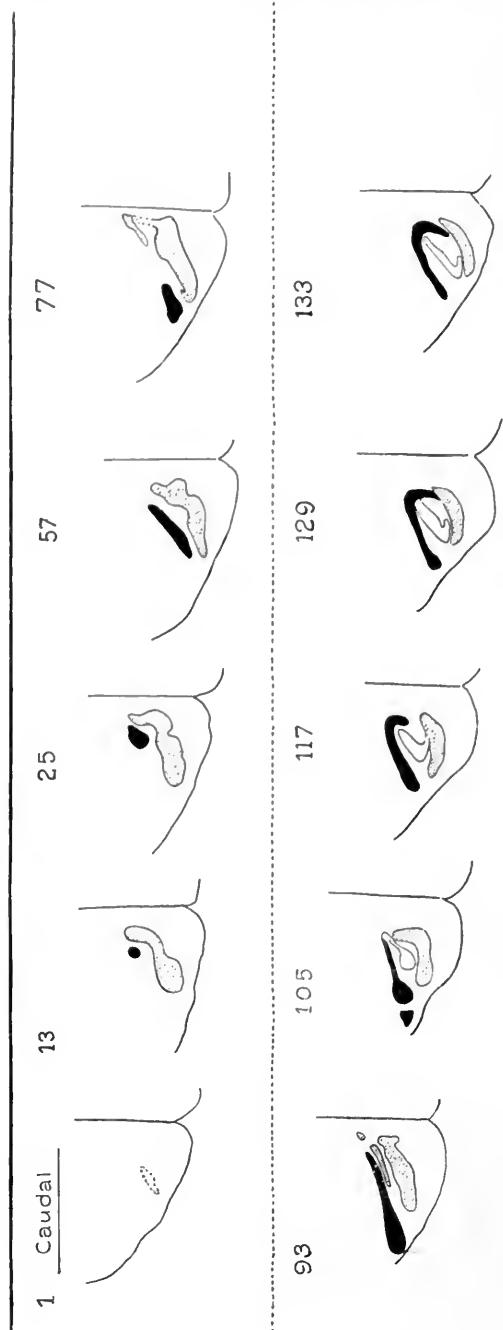


Table 50.
Abbreviated order of sections through the inferior olive of *Ilapate pennicillatus* E. Geoff.
Size of the section = 48μ .
Magnified $\pm 6 \times$.

The dorsal olive has a distinct V-shape; in caudal sections it has the usual form; sooner than in other Mammals, however, it bends around the medial top of the dorsal lamella. In most frontal sections it is connected with the medial lamella and remains present nearly until the frontal top of the olive-complex.

The ventro-lateral (principal) olive occupies about the frontal half of the olfactory complex.

Caudally the dorsal lamella is the first to develop; more frontally the medial one is even a little longer and bends ventrally into the medial oli-

ve. In most sections, however, the two olive-parts are separated.

Probably the free little nucleus, we find at that place in other Mammals, is the remainder of this bending part of the medial lamella.

The dorsal olive, which more frontally is about perpendicular on the medial lamella, is more frontally the dorsal continuation of this lamella (Table 50, s. 201—209).

In most frontal sections, the two lamellae melt together.

Cebus spec. — Table 51.

The medial olive can be divided into a big ventral component and a smaller medial one with a dorsal cap.

The angle between the two components is obtuse, as the ventral component is situated in the slanting plane, already described. The dorsal cap is connected with the caudal end of the principal olive and disappears more frontally (Table 51, s. 16—24).

The ventral component remains, of which the medial part is the

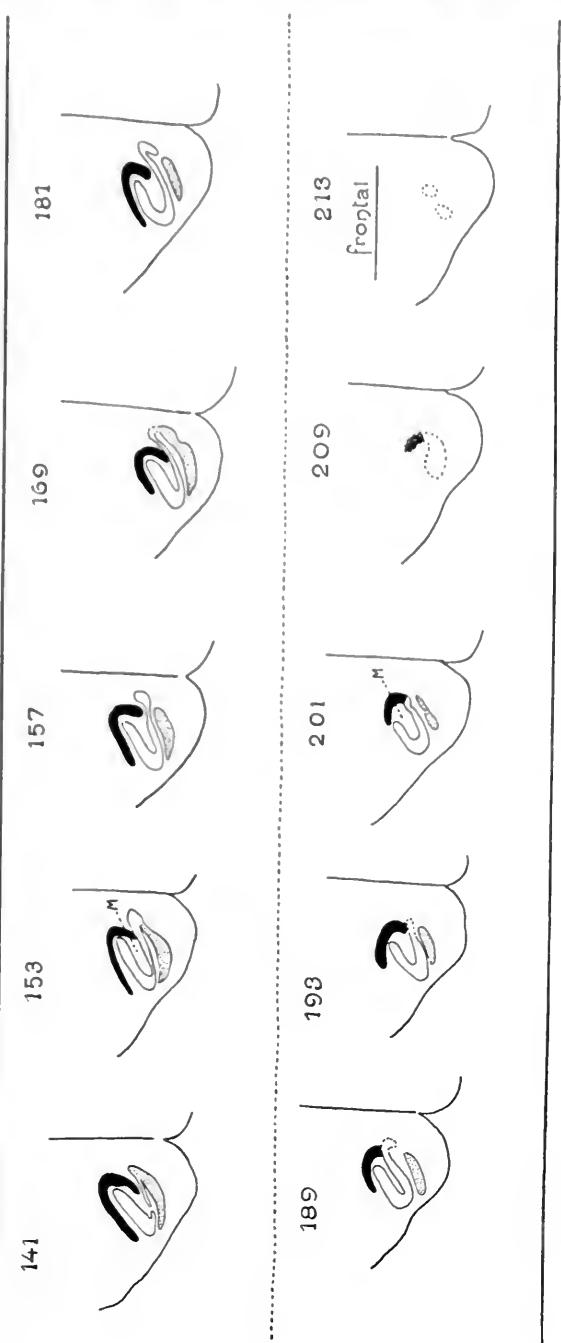


Table 50bis.

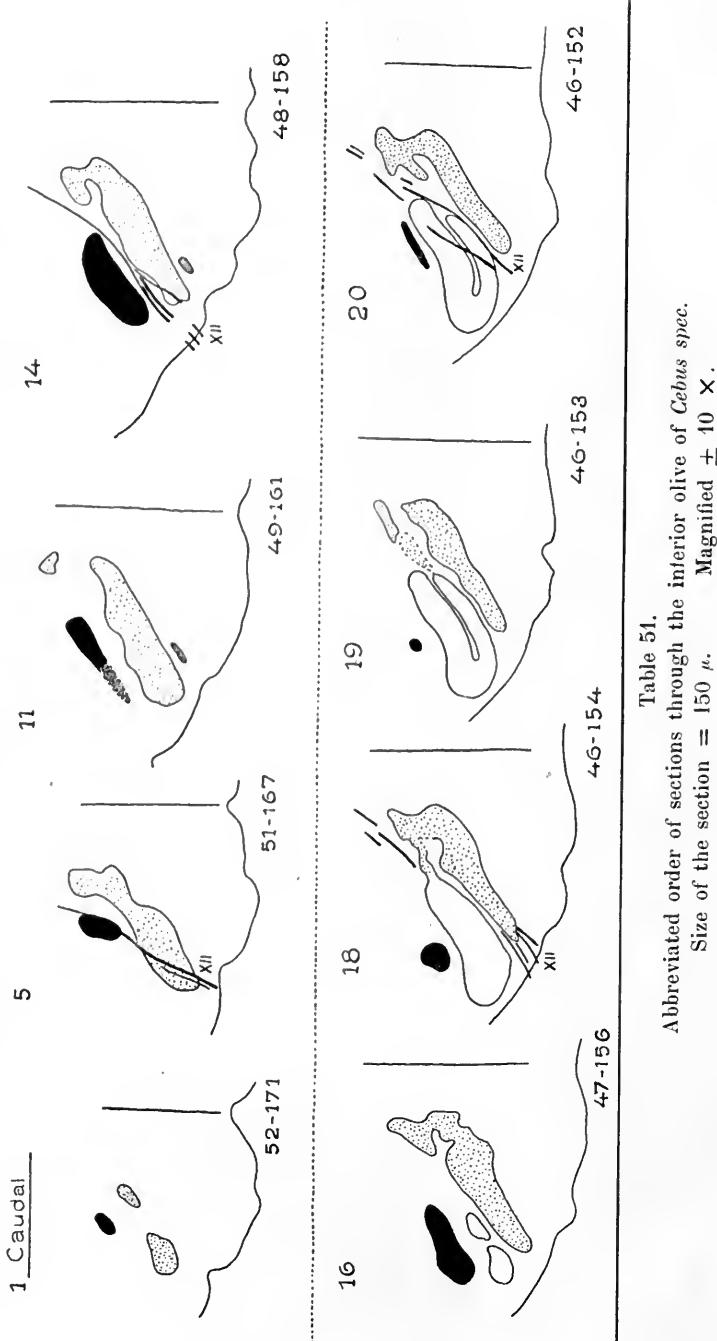


Table 54.
Abbreviated order of sections through the interior olive of *Cebus* spec.
Size of the section = 150 μ . Magnified $\pm 10 \times$.

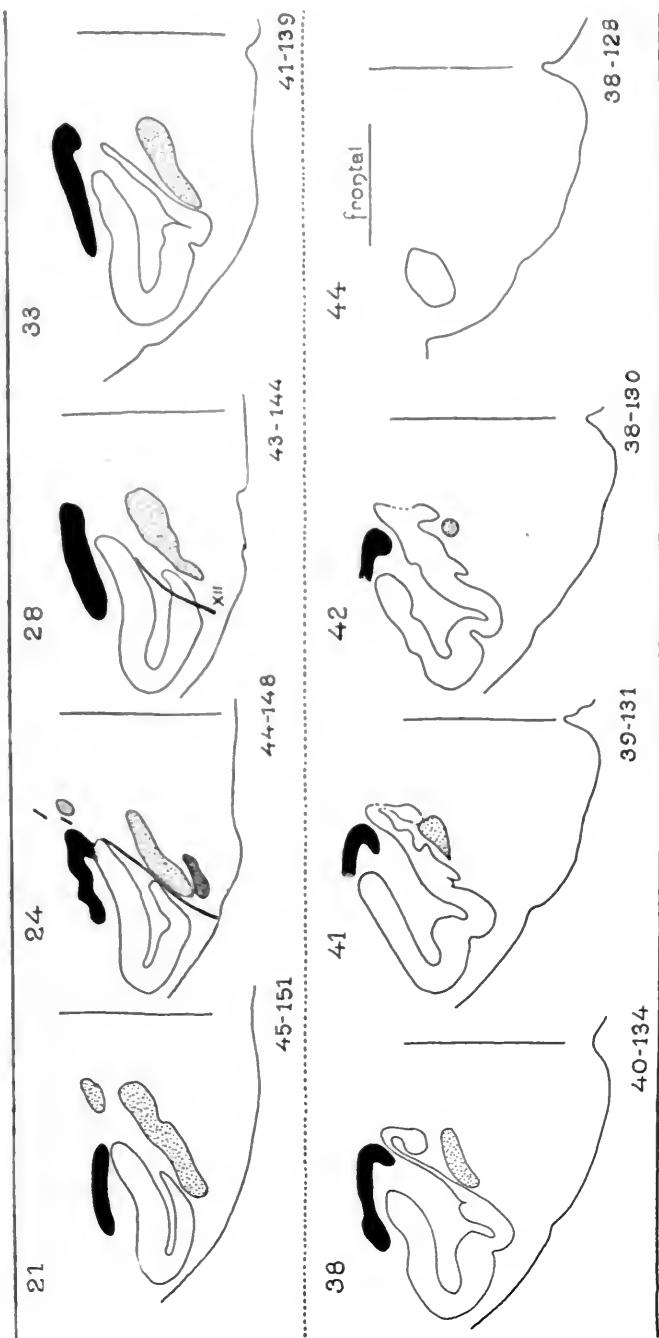


Table 51bis.

most frontal. In s. 11—14 (Table 51) and, more frontally, again in s. 24, small nuclei are visible, ventrally of the medial olive. They have no direct connection with the olive-complex I shall afterwards revert to them.

Speaking generally, the *dorsal olive* has the usual V-shape; in the caudo-frontal series of sections it can be seen that its position is successively dorsal, lateral and again dorsal. The ascending line of the V. has the wellknown flat shape. At the caudal appearance of the principal olive it almost disappears for a few sections (Table 51, s. 19, 20), but soon it becomes well-developed once more. In more frontal sections it blocks up the medial hilus and bends like a hook ventrally (Table 51, s. 33—42); it disappears exactly below the frontal top of the olfactory complex.

Beginning with *Cebus* the *ventro-lateral olive* becomes more and more important and fully deserves the name of principal olive. Not only does it occupy already 66% of the total olive-length in this primate, but also its transverse dimensions have considerably increased.

Both lamellae appear on about the same level and are first fused (Table 51, s. 16—19); like in other Mammals the dorsal lamella is, however, most important in caudal sections, being the longest (Table 51, s. 20—28) and till the most frontal sections also the thickest (Table 51, s. 19—41).

The hilus is well visible, the two ends, where it is closed, excepted.

The principal olive has a tendency to extend more and more laterally instead of ventro-laterally, as is also demonstrated by a groove in the dorsal lamella. On a more frontal level a distinct groove is visible in the connecting part of the two lamellae.

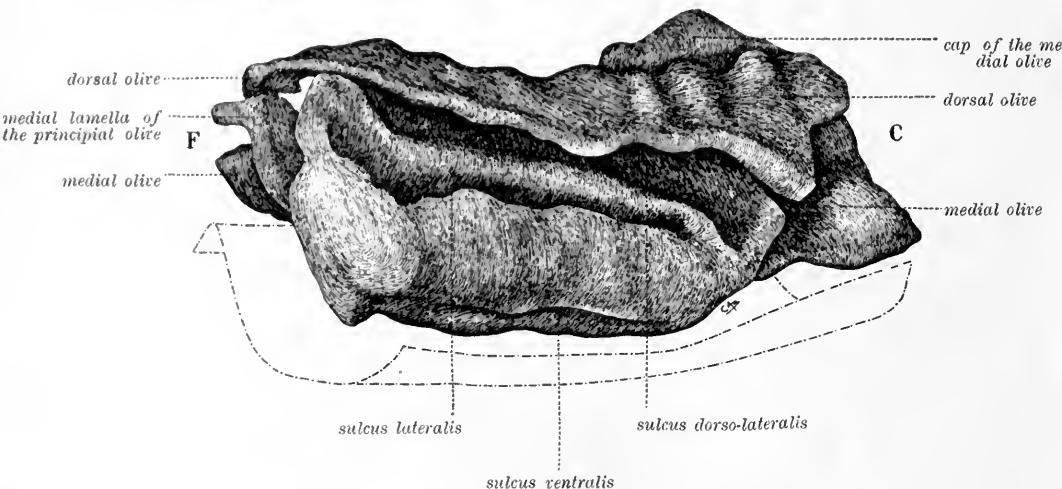


Fig. 88.

Inferior olive of *Cebus fatuellus*. — 16.5 × (fronto-lateral view).

The medial lamella, too, has a slight torsion in most frontal sections, while its dorsal top bends ventrally into the medial olive.

The two lamellae fuse and form the frontal top of the olfactory complex.

Cebus fatuellus. — Waxreconstruction: fig. 88, Table 52.

The medial and the dorsal olive are still well-developed, though they are far surpassed by the large principal olive.

The *medial olive* reaches most caudally; a division into a ventral and a medial component is possible; also the cap and a slight indication of the ventro-lateral outgrowth are present (Table 52, s. 18—22).

When the principal olive is well-developed, the medial one has become much smaller; more frontally it increases once more, to diminish

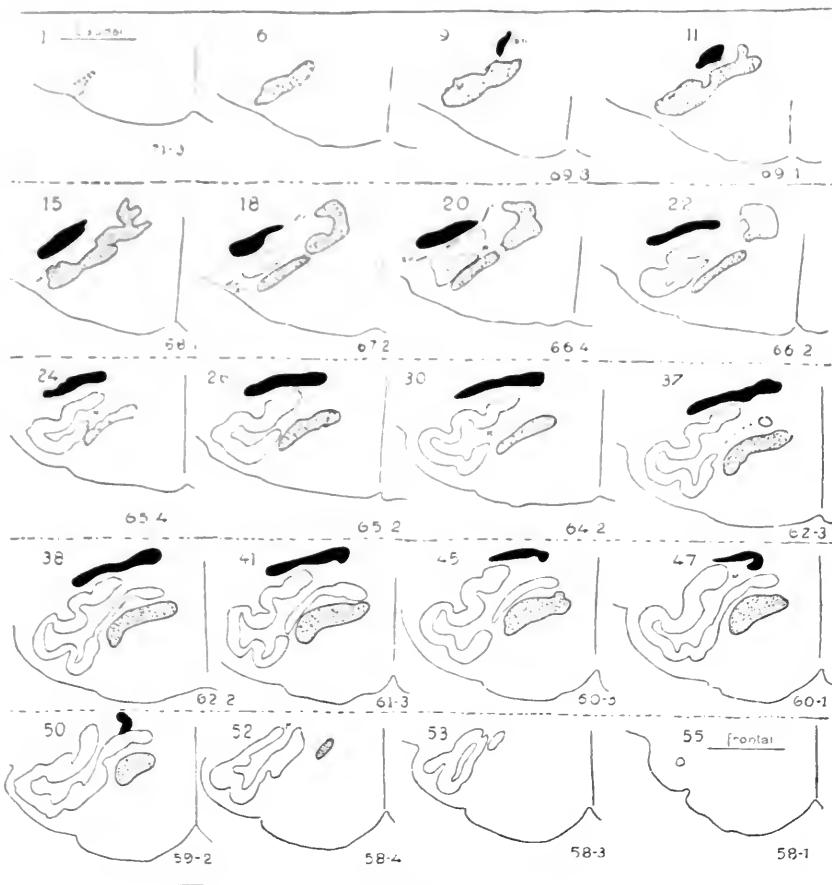


Table 52.

Abbreviated order of sections through the inferior olive of *Cebus fatuellus*.

Size of the section = 120 μ . Magnified $\pm 6 \times$.

and disappear on a much higher level (c. f. Table 52, s. 11—s. 24; s. 41—s. 52).

It is remarkable that the medial olive is nowhere connected with the principal olive.

The *dorsal olive* has a distinct V-shape, but the ascending line of the V. is much longer than the descending one, because of the principal olive reaching so far caudally (as we know, the dorsal olive again goes medio-dorsally at the caudal end of the principal olive).

During the presence of the principal olive, the dorsal one shows the plate-form.

The more one goes frontad, the more the dorsal olive gets a dorsal position; it bends round the medial top of the dorsal lamella, blocks up the hilus and finally touches the medial lamella (Table 52, s. 50).

It disappears a little below the frontal top of the olfactory complex.

The *ventro-lateral (principal) olive* is very well-developed. It occupies about 69% of the total length of the olfactory complex; the two lamellae fuse at their ends; caudally they appear on the same level (Table 52, s. 20) the dorsal one is longer and more sinuous.

It is remarkable, that the gyration is much stronger on a frontal level than on a caudal one.

I shall afterwards revert to the gyri and sulci, I only want to draw the attention to the fact, that they are all longitudinal and besides this, that there are two deep sulci (a ventral and a lateral one) and a more superficial lateral sulcus, dorsally of the deep one (see fig. 88).

Doubtless the most important gyrus is the one which is limited by the two above-mentioned deep sulci, viz: the sulcus lateralis and the sulcus ventralis (fig. 88); the convex surface of this gyrus is directed a little more laterally than ventrally. It was also this laterally projecting part, which seemed the most important of the principal olive in the former Cebus, as was the case with the ventro-lateral olive of nearly all Mammals, hitherto described.

There only remains to be remarked that on a frontal level the medial lamella is prolonged with a thickened dorsal end, bent a little ventrally (Table 52, s. 41—50), which is not in any section free from the principal olive, though not connected with the medial one.

Ateles hybridus Geoff. — Waxreconstruction: Fig. 89, Table 53.

The medial and the dorsal olive, though still better developed than in the highest Primates, more and more recede into the back-ground, when compared with the enormously developed principal olive.

Speaking generally, the *medial olive* is situated in the well-known slanting plane. A division into a ventral component and a medial one

with the dorsal cap is possible (Table 53, s. 28—69), but an outgrowth of the cap is not visible; the medial olive is free from the principal one, as well from its caudal end as, more frontally, from its medial lamella.

The most frontal part of the medial olive corresponds to the angle between the two components (Table 53, s. 81—115). It disappears rather far below the frontal olive-top (Table 53, s. 115).

Like in *Cebus fatuellus*, in a few sections, a reduction is visible on the level of the caudal end of the principal olive (c. f. Table 53, s. 15—53—75).

The dorsal olive shows a distinct V-shape, but the ascending line begins when the principal olive is already fully developed. As can be seen in fig. 89, there is a great difference between the caudal part, which is about round, and the plate-shaped frontal part.

In *Ateles*, the beginning of a separation between the two indicated parts can probably be seen as an introduction of the condition, found in highest Primates, where they are separated by a large interval.

The frontal part of the dorsal olive is well-developed; it covers, however, only the medial half of the dorsal lamella,

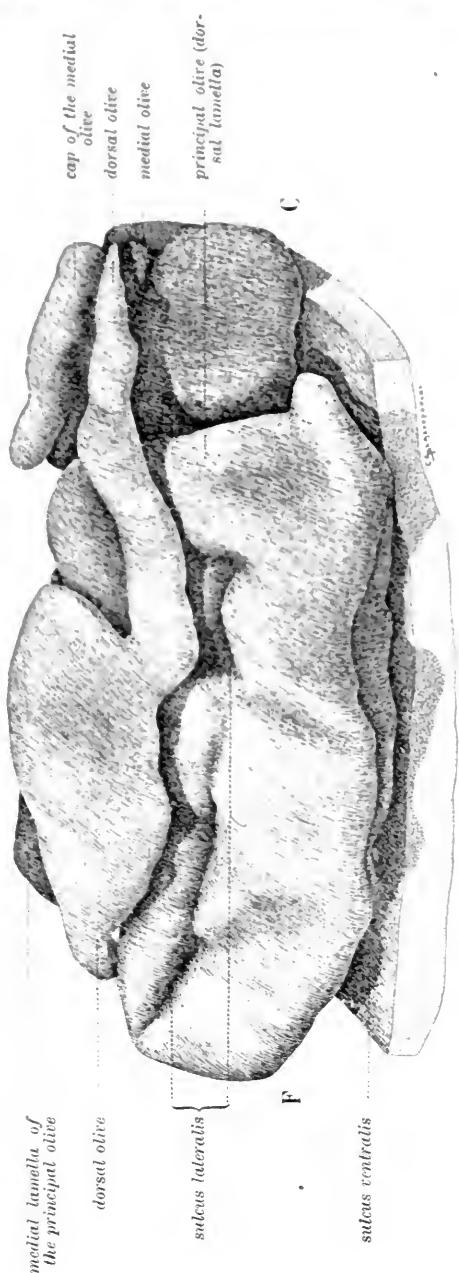


Fig. 89.
Inferior olive of *Ateles hybridus* Geoff. - 43.3 X (lateral view).

perhaps because of the strong ventro-lateral development of the principal olive.

Still more frontally, the dorsal olive bends round the medial top of the dorsal lamella and blocks up the hilus. It does not get connected

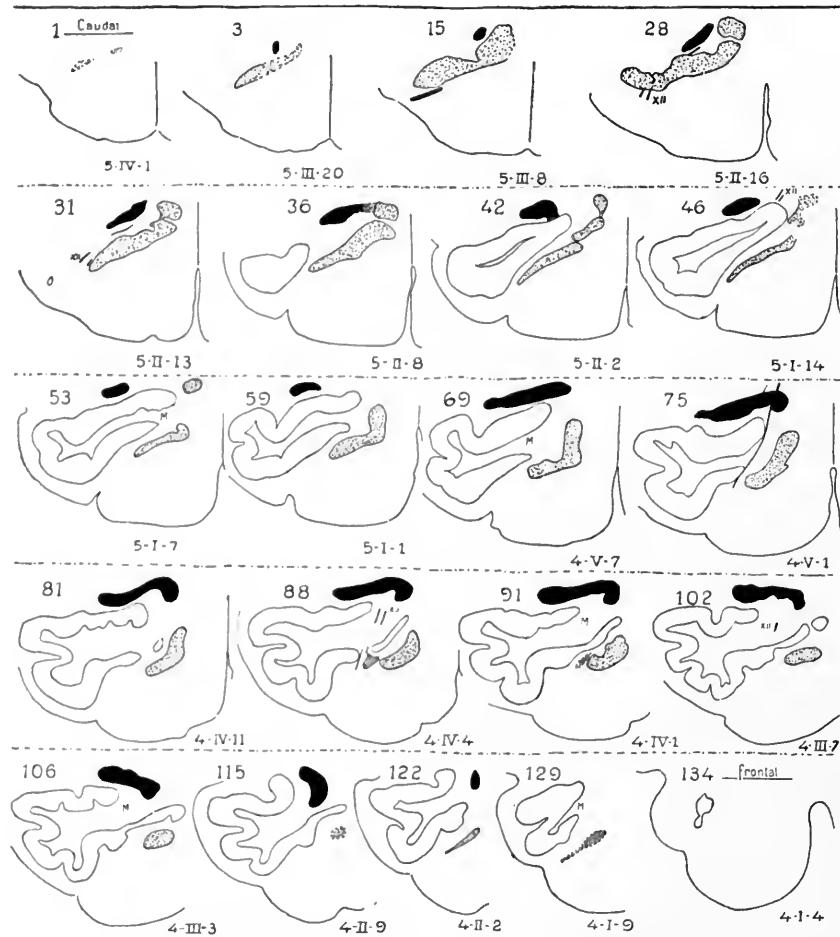


Table 53.

Abbreviated order of sections through the inferior olive of *Ateles hybridus* Geoff.

Size of the section = 60 μ . Magnified $\pm 6 \times$.

with the medial lamella and disappears a little below the frontal top of the olfactory complex.

In its caudal sections, the principal olive resembles that of *Cebus fatuellus* very much; caudally the two lamellae fuse (Table 53, s. 36—46) and get free on the same level. Then the medial hilus remains well

visible unto the frontal top, where the lamellae are united once more (Table 53, s. 134).

Also in Ateles, the dorsal lamella is the longest over the greater distance, whereas the medial lamella becomes long on a more frontal level, showing a thickened medial end. Like in *Cebus fatuellus*, the dorsal lamella is most sinuous, while also here, the convolutions are more numerous frontally than caudally.

The deep lateral and ventral grooves are also present in Ateles and limit an analogous lateral gyrus; the superficial lateral groove of *Cebus*, however, is absent. On the contrary, we find in Ateles a ventral gyrus, which we did not see in *Cebus* and which is well-developed, especially in frontal regions. It is bordered by the above-mentioned ventral groove and a medio-ventral one in the medial lamella (Table 53, s. 75—129). Over some distance (Table 53, s. 88—115), this gyrus is even divided by shallow sulci into two or three (Table 53, s. 102) smaller convolutions.

Like in *Cebus fatuellus*, the sulci and gyri are quite longitudinal, only the lateral sulcus is interrupted by a bridging-convolution (see fig. 89), a phenomenon, which we shall see more and more in higher Primates.

Anthropopithecus troglodytes L. — Waxreconstruction: Figs. 90 and 91, Table 54.

In *Anthropopithecus troglodytes*, the principal olive is so much en-

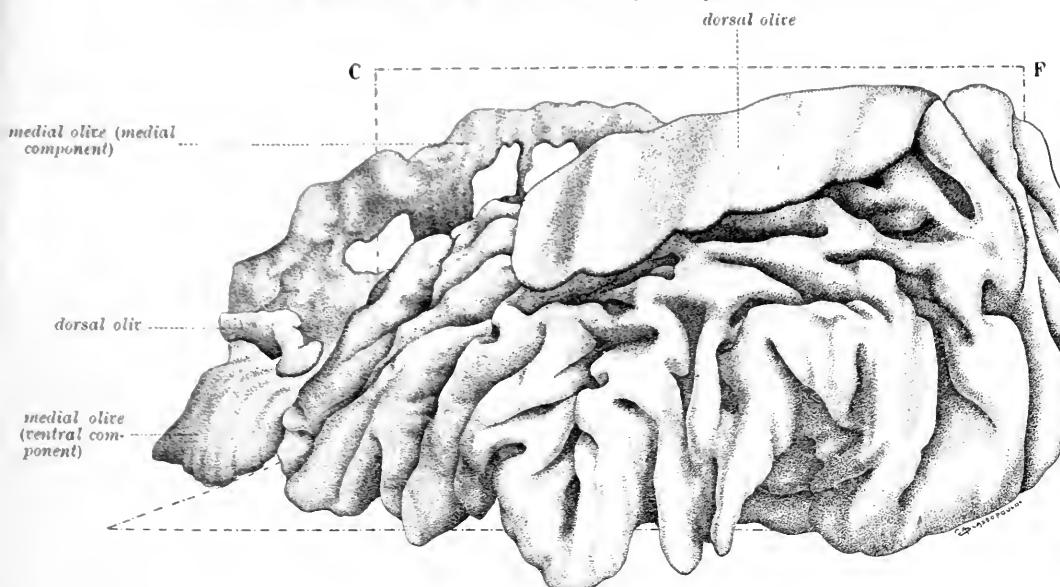


Fig. 90.

Inferior olive of *Anthropopithecus troglodytes L.* — 13.3 × (lateral view).

larged, that the medial olive and the dorsal one quite deserve the name of accessory olives.

Yet the form of *the medial olive* in lower Mammals can be found again in that of the monkey in question.

Caudally it is the first of the three olive-parts to appear, its ventral component reaching rather far laterally. The medial component, appearing more frontally, (the division into the two components is very clear in *Troglodytes*) shows a dorsal cap and a ventro-lateral outgrowth; the latter is indistinct in nearly all sections and, like the dorsal cap, it is for the greater part a free small nucleus (Table 54, s. 20—26).

Therefore the interpretation is only possible by comparing it with the Mammals, already described.

When cap and outgrowth disappear, a medial strip remains, of which only the dorsal point is well-defined (Table 54, s. 30—45), but a little higher (Table 54, s. 47), the medial olive increases once more. On about the same level, a small strand of cells appears medially (Table 54bis, s. 52)

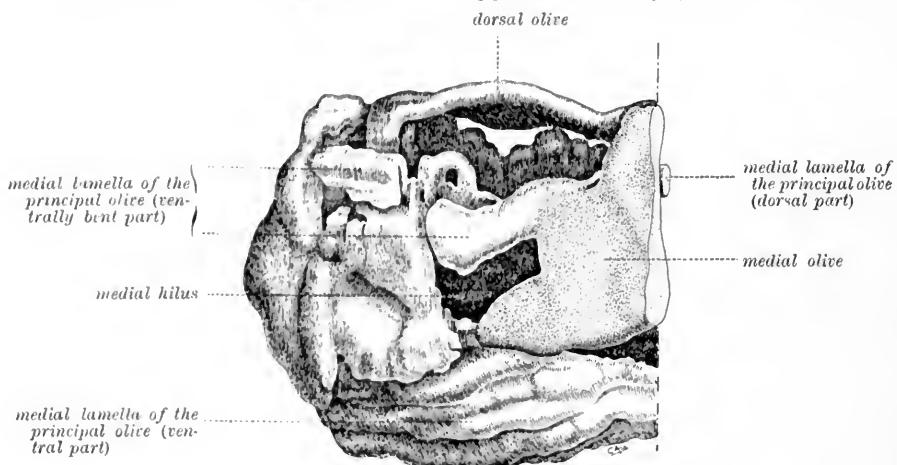


Fig. 91.

Frontal part of the inferior olive of *Anthropopithecus troglodytes L.* (medial view).

of the medial olive, which soon reaches rather far ventrally. Very probably this nucleus corresponds to the dorsal part of the medial lamella in lower Mammals, which already showed its tendency of getting free in *Ateles* and *Cebus fatuellus*. In *Troglodytes* it is not at all connected with the medial olive and only indistinctly with the medial lamella of the principal olive (Table 54, s. 75—79). The above-mentioned decrease of the medial olive after the cap has disappeared, and its enlarging once more, is also described for other Mammals (*Elephas*, *Cebus fatuellus*, *Ateles hybridus*).

Another thing is, that in *Troglodytes*, the medial olive has a more

dorsal position than in lower Mammals, probably in consequence of the large development of the pyramid, whereas the principal olive can extend freely ventro-laterally. So the situation of these two olive-parts has altered with regard to each other.

The medial olive disappears rather far below the frontal top of the olfactory complex (Table 54, s. 72).

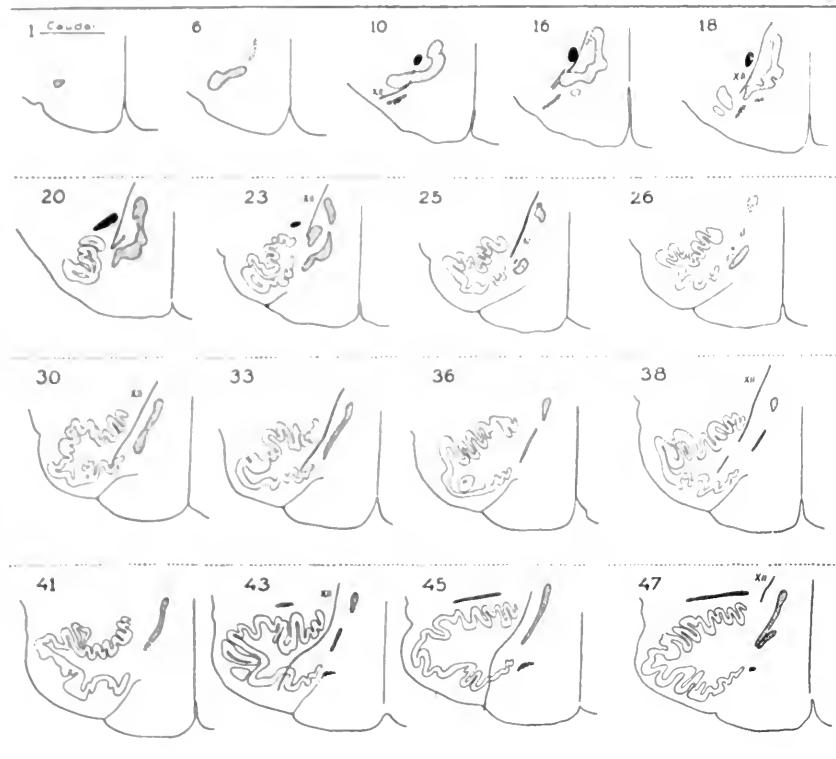


Table 54.

Abbreviated order of sections through the inferior olive of *Anthropopithecus troglodytes L.*

Size of the section = 120μ Magnified $\pm 3 \times$.

Caudally, the dorsal olive shows the same position as in other Mammals, viz.: dorso-laterally of the medial olive, while its form in transverse sections is about round. It becomes flatter at the caudal appearance of the principal olive and disappears in the following sections (Table 54, s. 23), to appear once more on a higher level (about s. 43), lying like a thin plate on the medial part of the dorsal lamella. Still more frontally, it bends round the medial top of this lamella, blocking up the hilus of the principal olive.

Both accessory olives end frontally at a greater distance from the top of the olfactory complex than is the case with lower Mammals.

The principal olive has developed enormously. It occupies about 81% of the total olive-length, but still more striking is its extension in a ventro-lateral direction; this is first shown by the protrusion, it makes on the border of the bulb, but its surface is still more enlarged by its being exceedingly lamellated.

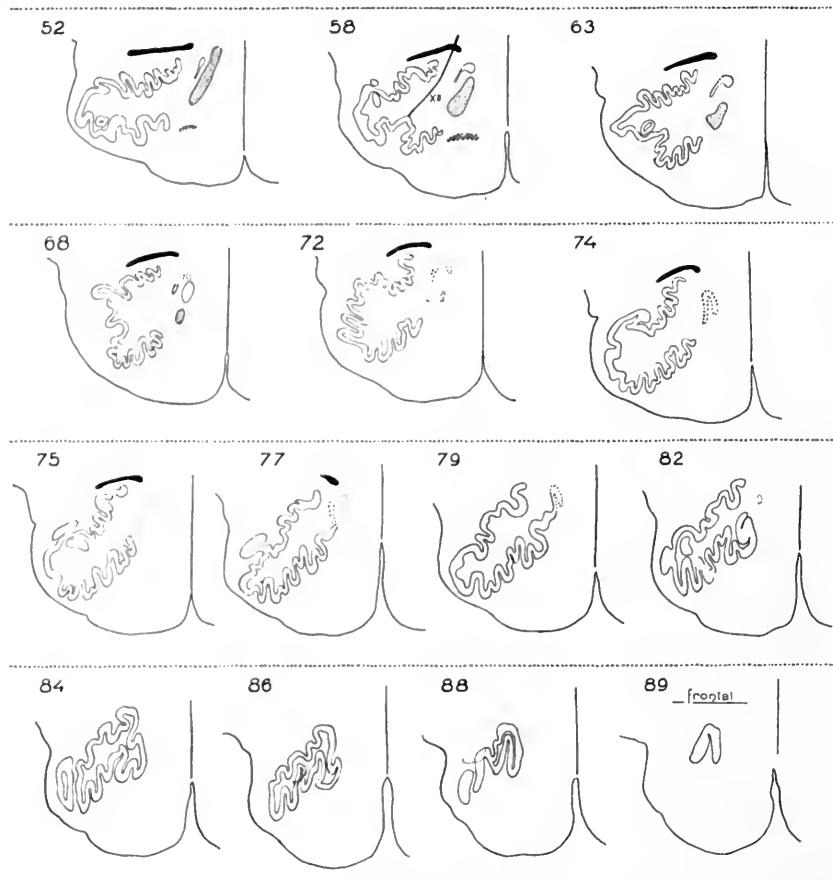


Table 54bis.

I shall afterwards revert to these gyri and sulci, suffice it to say, that the principal olive gradually extends more ventro-laterally¹⁾ when examined from caudally to frontally, until about the middle, where it

Note 1: In the model the farthest ventro-lateral protrusion is seen in the caudal half of this olive-part.

gradually begins to diminish, to disappear more rapidly at the frontal end (Table 54, s. 89).

The dorsal lamella is the largest and the most lamellated, but for the more frontal sections, where the medial lamella too, is well developed and its sulci become more numerous and deeper. This tallies quite well with the properties I found for that lamella in lower Mammals: its being long, and in Ateles, its being lamellated only on a frontal level.

I have already described the indistinct small nucleus, interpreted as the dorsal part of the medial lamella (*vide supra*).

Conclusions.

In the olfactory complex of all Mammals we could distinguish three parts: a *medial*, a *dorsal* and a *ventro-lateral* one.

First of all must be decided whether these three parts are really identical from Marsupials unto the highest Primates.

It is indeed possible to compose a scheme, valid for the medial olive and for the dorsal one in all Mammals.

The following characteristics can be found again in the various medial olives:

1. The *medial olive* reaches *farthest caudally*.
2. Most caudally we see only *its ventral component*, which is at the same time *the most lateral part* of the medial olive.
3. On its ventral surface a *groove* is more or less distinctly visible. According to this groove being deep or shallow, the medial olive gives the impression of being sinuous or more compact.
4. A little more frontally also a *medial component* is present; the two components are sometimes placed perpendicularly on each other (Ungulates); generally, however, they form an obtuse angle and represent the shape of a comma.
5. Still more frontally the medial component shows a *dorsal cap*.

On that level there is a rather great difference in the morphology of the various medial olives, caused, however, by the changes which the principal olive undergoes during its phylogenetic development. In lower Mammals (*Didelphys*, *Erinaceus*) the ventro-lateral or principal olive is connected with the medial one almost over its total length, though most intensively in caudal sections, whereas in higher Mammals this connection is chiefly confined to those caudal sections. When the principal olive, developing enormously, has at the same time become entirely independent from other parts, of this caudal connection only the ventro-lateral outgrowth of the medial olive remains (*Elephas*, *Anthropopithecus troglodytes*).

I had to anticipate, as I was obliged to discuss the principal olive, in order to explain some differences in the medial ones, which existed only apparently. The same is the case with the more frontal sections through the medial olive.

In lower Mammals, the medial lamella of the principal olive bends ventrally and becomes connected with the medial olive. When, however, in higher Mammals, the principal olive becomes free, as mentioned above, this connection too, disappears.

It is characteristic of all olive-parts, that they become quite free, when fully developed. So the frontal part of the medial olive in Cetacea is enormously developed, as will be remembered, and at the same time quite free (surrounded by a thick fleece of fibres), even from the rest of the medial olive. Now Cetacea, though apparently having a special position of their own, do not really interfere with the general scheme. The caudal part of their medial olive follows the scheme exactly: a similar ventral position, the same grooves as in Ungulates, the dorsal cap and its ventro-lateral outgrowth; the frontal part of the medial olive differs only apparently from the analogous part in other Mammals, but it has the same medial position and only is much larger.

Speaking of the frontal part of the medial olive, I return to my scheme.

6. When the principal olive has appeared caudally, the medial olive is more and more restricted to its medial part.

Sometimes, it is clearly the medial component which remains present, more often, however, the place of the frontal part corresponds to the angle between the two components more below. At any rate, it takes a medial position, while the principal olive lies at its former lateral place. I have already told that in those frontal regions it is often connected with the medial lamella of the principal olive.

Resuming I refer to the scheme of table 55, in which are drawn 5 stages, following each other in caudo-frontal examination, thus:

Stage 1. The medial olive reaches most caudally, at the same time stretching rather far laterally.

Stage 2. It extends especially in a medial direction; a ventral groove is generally visible; a division into a ventral and a medial component is often possible.

Stage 3. The medial olive shows a dorsal cap and begins to disappear in medial direction at the caudal appearance of the principal olive.

Stage 4 and 5. The cap has disappeared; the medial olive has a quite medial position and becomes smaller and smaller; it disappears — (perhaps with the exception of the very low Mammals) — caudally to the frontpole of the olfactory complex.

The dorsal olive. This olive-part too, has about the same form in the series of various Mammals. Speaking generally it has, when modelled, a V-shape. Of this V, the highest point of the descending line is the most caudal and at the same time the most dorsal point of the dorsal olive, whereas the lowest point of the descending line corresponds to its most lateral position and lies on the level of the caudal end of the principal olive.

Now this descending line need not to be straight; its different forms are schematically represented by lines in Table 56. In *Halicore* it extends horizontally over a great distance and then rather abruptly makes the V-figure.

Just the contrary is the case with *Macropus*; almost immediately at its caudal beginning it goes laterad and keeps this lateral position till the caudal appearance of the principal olive.

Canis familiaris shows a more gradual descent, which is the usual case: most caudally the dorsal olive remains over a short distance in its dorsal position; then it gradually goes laterad.

Also *Lepus cuniculus* shows this gradual descent; the so different

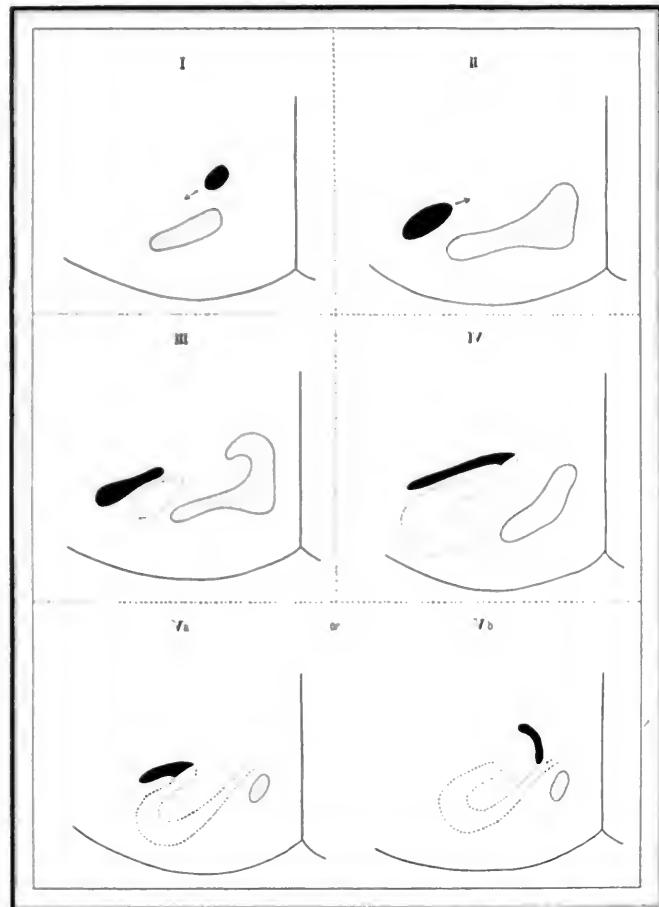


Table 55.

Frontal.

Scheme, showing the form and position of the medial and the dorsal olive on different levels, as seen in a cando-frontal examination.

incline of the descending line of the V in *Canis* and *Lepus* is caused by the different stage of development of the principal olive.

As in lower Mammals the latter does not reach so far caudally as it does in higher ones, and as the most lateral point of the dorsal olive coincides with the caudal end of the principal olive, it is evident that this lateral point is situated much more frontally in lower Mammals than in higher ones. Moreover the incline is dependent on the question how far the lowest point of the V reaches laterally. Finally it is influ-

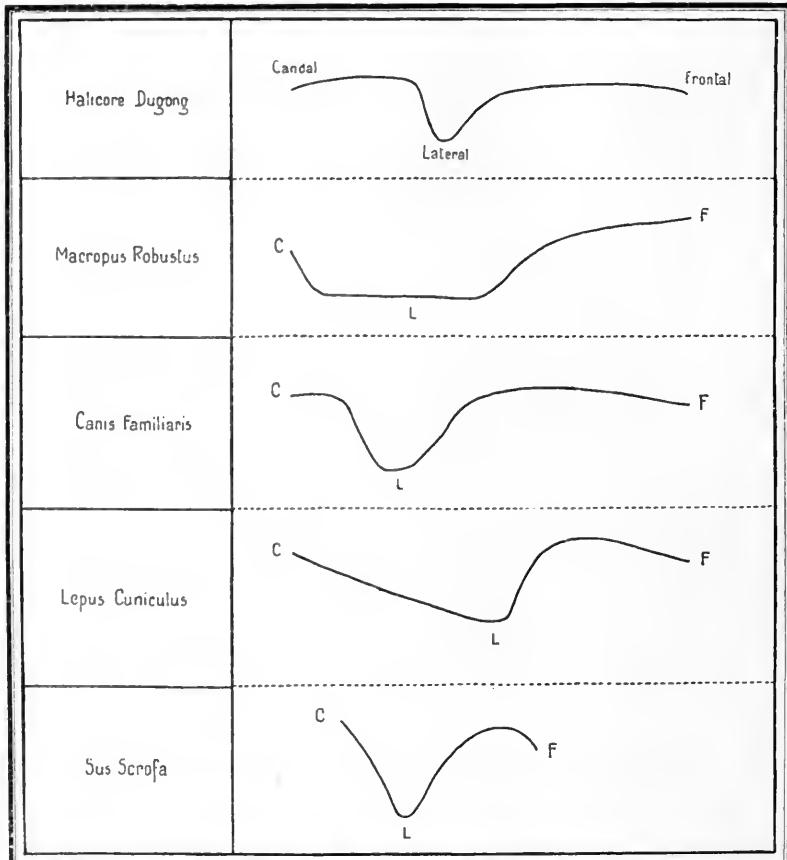


Table 56.

Scheme, showing the different V-shapes of the dorsal olive in various Mammals.

enced by the more or less compactness of the total olive: so in *Sus* and *Phoca* the dorsal olive has a very sharp V-shape, because of its being so compact in those animals (Table 56).

I dwelled at length upon those differences, not because of their

importance, but on the contrary to show that notwithstanding them, the same principle of the V-shape can be found again in all Mammals.

The coincidence of the beginning of the ascending line and the caudal end of the principal olive includes the fact, that with the enlargement of the principal olive in higher Mammals, also the ascending line increases (compare f. i. *Lepus* and *Canis*).

The ascending part, which is always flat, covers the dorsal lamella of the principal olive and more frontally bends ventralward.

It becomes often connected with the dorsal lamella, especially in lower Mammals (*Insectivora*, *Marsupialia*, *Edentata*) or bends still more ventralward, blocks up the medial hilus and touches the medial lamella of the principal olive or becomes connected with it.

Table 55 shows the 5 stages schemetically.

Now it is easily understood that, on account of the above-mentioned dates, I was also able to interprete the badly defined dorsal olive in lower Mammals.

For also in *Didelphys* and *Erinaceus* this scheme can be found again: *caudally* the dorsal olive has a *dorsal position*;

more frontally its position becomes *more lateral*;

at the caudal appearance of the ventro-lateral extension (= principal olive) *it returns medio-dorsalward, at the same time becoming flat.*

(See also the slight V-shape in fig. 68 and that of the dorsal olive in *Erinaceus* fig. 70).

As has already been mentioned, the ascending line of the V-figure becomes the most important in higher Mammals; of this dorso-lateral plate the medial part is the most important, especially on a frontal level. When in higher Primates the principal olive develops more and more, only the medial part of its dorsal lamella is covered by the dorsal olive, as the latter has not kept pace with the enormous growth of the principal olive (perhaps also the lateral part of the dorsal olive has atrophied a little). In *Ateles hybridus* a piece of the dorsal olive seems to have fallen away, so that a division into a caudal and a frontal part exists. In *Anthropopithecus troglodytes* this gap is complete, so there the two parts are quite separated (see Table 54, fig. 90). As all parts have become free from each other in *Anthropopithecus troglodytes*, also the frontal end of the dorsal olive is in no way connected with any of the lamellae.

The ventro-lateral (or principal) olive.

This is the part which differs most in the various Mammals. Yet it can be found in all of them and certainly they are all analogous.

First, we found everywhere three parts, situated: medially, dorsally

and ventro-laterally. A priori it is very probable that, where the two first mentioned parts are certainly identical, also the parts mentioned sub 3, placed in the same way with regard to the others, will prove to be analogous.

But moreover there are the same characteristics:

1°. the ventro-lateral (principal) olive reaches nowhere most caudally but always most frontally.

2°. in all Mammals it shows (more or less) two lamellae, a dorsal and a ventral one, forming a hilus which opens medially.

3°. the dorsal lamella is the most important; only in the highest sections through the olive the medial one is well developed.

If those points of resemblance are not yet sufficient, all doubt is taken away by studying the series of Primates from high to low. Compare the figures 90, 89, 88, 87 and the Tables 54—49, in which the

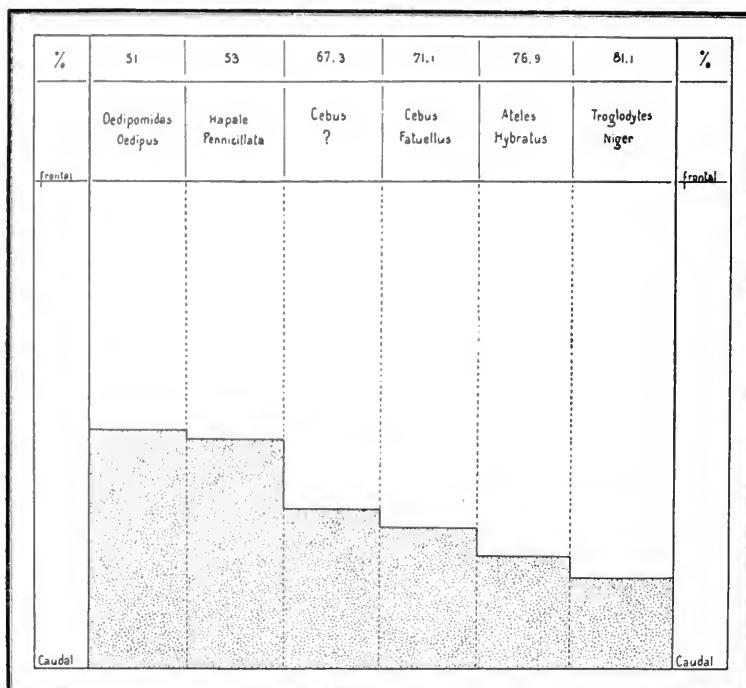


Table 57.

Scheme, showing the growth of the principal olive in Primates, in the caudo-frontal dimension.

The distance between the lines, indicated by frontal and caudal, represents the total olive-length. The length of the principal olive is represented by the space, left white, whereas the caudal rest of the space, where the medial olive is present only, is finely dotted.

principal olive can be seen gradually reaching less caudally and becoming smaller. Its lamellae become less winding, till they are without any sulcus, and are finally only well developed in a few sections (Table 49, s. 40—43) and more closely connected with the other olive-parts.

Less gradual, but similar is the decline in the development of the principal olive throughout the series of Mammals below the Primates, unto Didelphys.

After having ascertained that the ventro-lateral olivepart is identical in all Mammals, we can summarize its development in inverse order, from Didelphys to *Anthropopithecus troglodytes*.

This development takes place in all dimensions:

19. in the caudo-frontal dimension, chiefly in a caudal direction.

As fixed points I have taken the poles of the medial olive because of their being the least changed in the whole series of Mammals. This caudal direction of the development is also given by the most lateral point of the dorsal olive migrating caudally.

Only in the very high Primates the principal olive has also grown

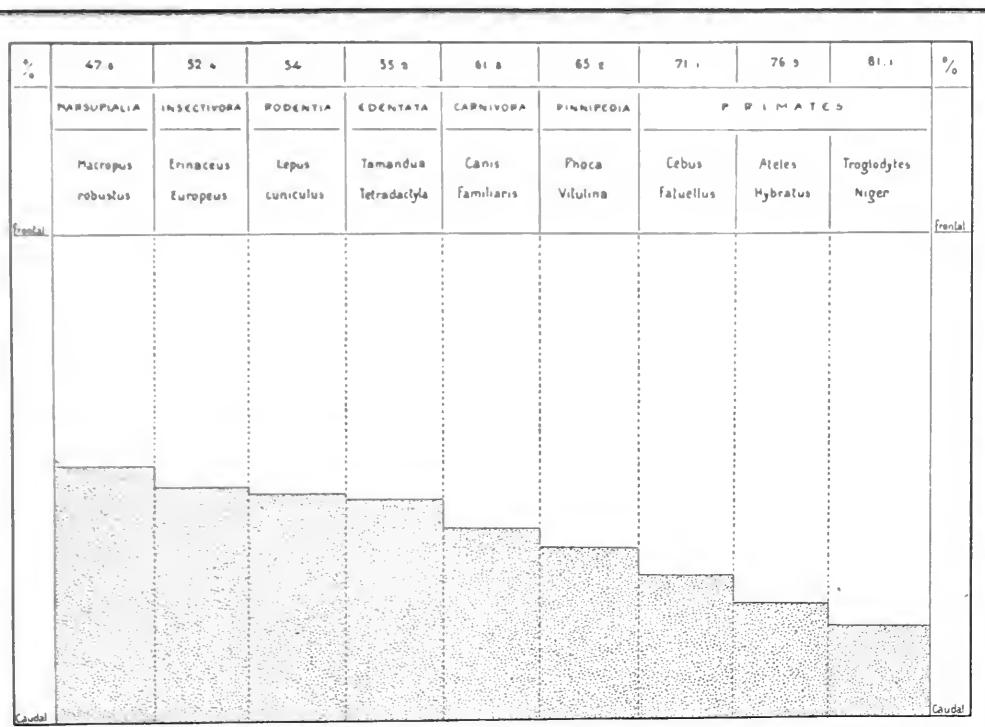


Table 58.

Scheme, showing the growth of the principal olive in Mammals, in the caudo-frontal dimension.

in a frontal direction, even in regard with the dorsal one, at least if we do not suppose that the latter has atrophied.

The fronto-caudal development in Simiae can be seen in Table 57, that

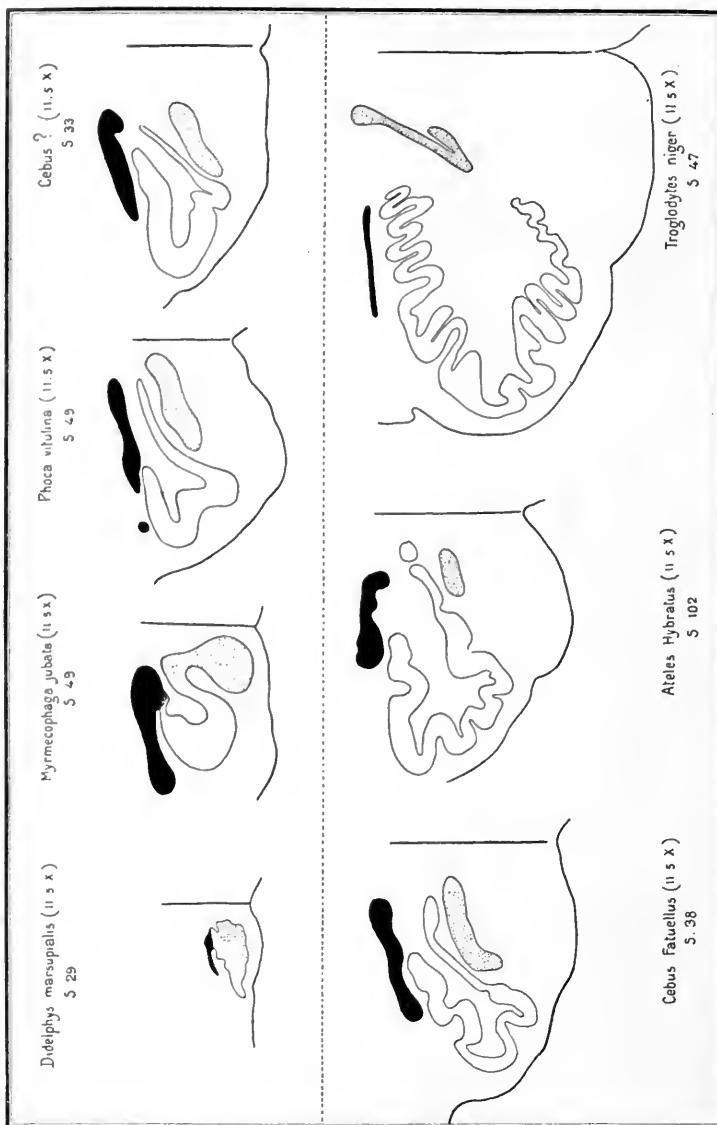


Table 59, showing sections through the olives of various Mammals on a level, where the principal olive is developed best.

in the whole series of Mammals in Table 58. The very regular enlargement, which is represented in the latter Table, is, however, exaggerated. Exceptions occur, some easily understood, others, which cannot be explained. The

principal olive in Ungulates f. i. occupies only 50% of the olive-length; perhaps the two other olive-parts, which in other dimensions are so well developed, are also longer than usual and so diminish the percentage of the olivepart in question.

This is certainly the case with Cetacea with their enormously developed medial olive; in *Tursiops* f. i. the principal olive occupies only 48% of the total olive-length, whereas the same part in *Elephas* occupies 74% because of its dorsal lamella being greatly hypertrophied.

So table 58 shows the undeniable enlargement of the ventro-lateral (principal) olive in the phylogenetic series only schemetically.

29. In the other dimensions the development is not less evident. Being in lowest Mammels only a compact ventro-lateral outgrowth, the principal olive shows in higher animals the two well-known lamellae, which become larger, at the same time extending ventro-laterally and causing a protrusion in the border of the bulb. When a still larger surface is wanted, these lamellae become gyrated and also here we see the tendency of an extension in latero-ventral direction, for the lateral lameilla is the first to show sulci and is in highest monkeys the most gyrated (the first gyrus is directed ventro-laterally).

The sulci in the medial lamella are both less deep and numerous, more-over chiefly present on a frontal level.

Table 59 shows the development of the principal olive. The sections of this table cut the olive-part in its full size; for an exact study, however, the whole tables are necessary.

30. As has already been mentioned above, the lamellae not only enlarge, but also get more and more distinct, and so does the medial hilus (e. f. *Didelphys*-*Myrmecophaga*-*Phoca*, Table 59).

40. The ventro-lateral olive becomes independent from other parts.

In lower Mammals it is connected with the dorsal tops of the other olive-parts, of which we find in highest animals only a reminiscence in the bending-ventrally of the top of the medial lamella.

But also the close connection between the caudal end of the principal olive and the medial one becomes less intense, while the connecting point at the same time shifts caudally.

Finally, only the ventro-lateral outgrowth of the dorsal cap remains, though often very indistinct (Table 60; this table also shows that the dorsal lamella reaches farther caudally than the medial one and is free from the medial olive over a greater distance, *Canis familiaris*).

It is here the place to refer to the publications of Kankeleit (1913) and Williams (1913).

I have often spoken of the „Vierblättertypus” of Kankeleit; this

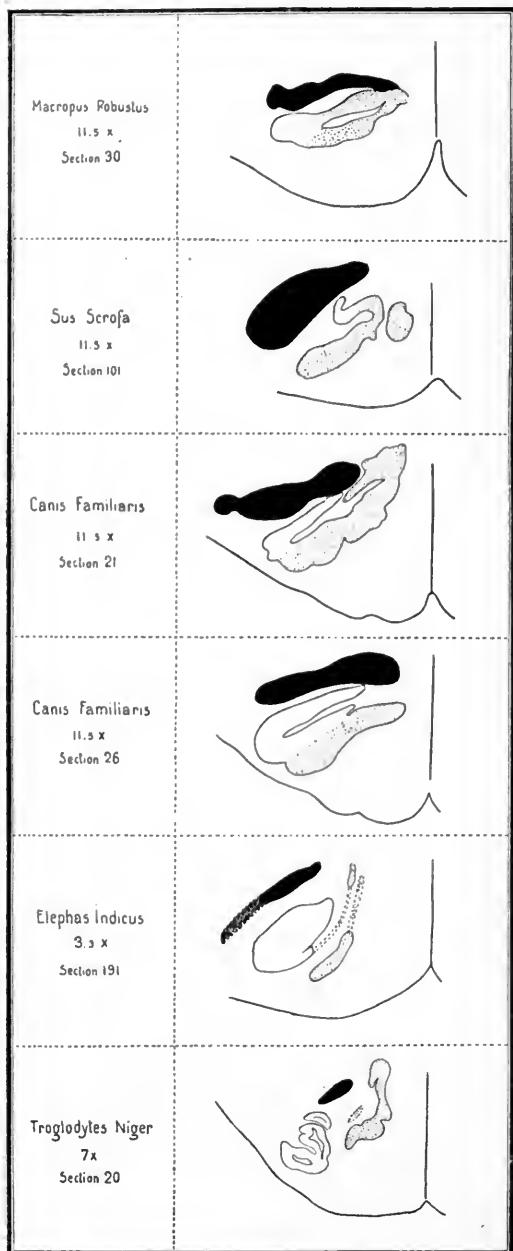


Table 60,
showing sections through the olives of various
Mammals, on the level of the caudal
appearance of the principal olive.

author considers the two inner lamellae to be analogous with the principal olive and the outer ones with the accessory olives in Man. I have already explained why I agree with him in this point.

It is a pity, however, that he compares only certain levels of the inferior olives, for now the proper arguments for his interpretation are wanting, as has appeared from the models and tables.

Williams, who also considered the lower sections through the olive, as often described a lateral as a medial hilus and for the same reason did not always see the four lamellae. In caudal sections, especially in lower Mammals, the lateral hilus is indeed far and away the most important (f. i. in *Macropus*); in several of those primitive Mammals the four lamellae are nowhere to be found, the medial hilus being slightly indicated.

So the difference between Kankeleit and Williams may be explained by their studying different levels. In my opinion, however, Kankeleit's interpretation of the olive-parts in the sections he described, is right.

Hypothesis of the growth of the principal olive during phylogenesis.

It seems very probable that the medial olive, which in all orders of Mammals has the same form, is an old part in comparison with the ventro-lateral one, which may be a younger part, as it changes so much during phylogenesis.

In the lowest Mammals the ventro-lateral olive is not only poorly developed, but also closely connected with the medial olive; in higher Mammals it has become well-developed and independent from the latter.

While the ventro-lateral (or principal) olive develops caudalward, its point of connection with the medial olive also shifts caudal.

These three points make it very probable that the principal olive has developed out of the lateral surface of the medial complex, by some influence, as yet unknown, beginning to grow out at the frontal top of the latter.

During phylogenesis the same reason obliged the outgrowing part

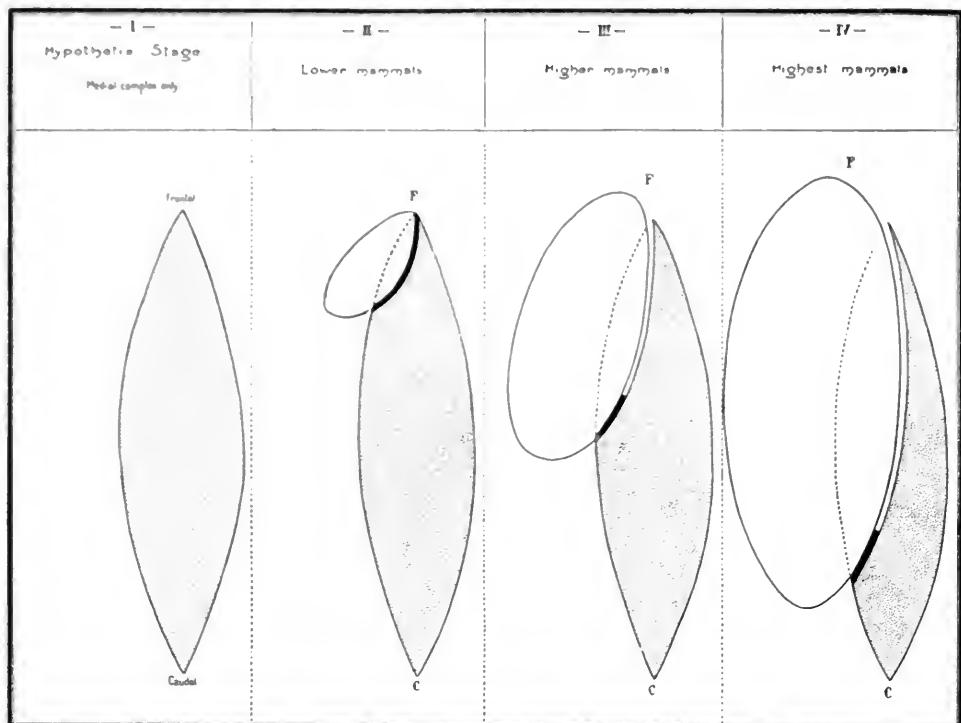


Table 61.
Scheme, showing the growth of the principal olive in Mammals.

to develop further in a caudal and at the same time ventro-lateral direction, while its frontal part, which grew out first, became entirely independent from the medial complex.

In this way the three above-mentioned points are easily understood. Also the fact that the lateral lamella of the principal olive shows the greatest development and reaches farthest caudally, whereas its medial lamella is only well developed in frontal regions, can be explained with the help of this theory. For because of the caudal and lateral direction of the growth, the lateral lamella must precede in development (see f. i. *Canis familiaris*, Table 60).

The theory is schematically represented in Table 61. In order to show the course of the development I have first drawn a hypothetical stage in which only the medial complex is present, out of which the medial and the principal olive will differentiate.

The stages 2—4 represent the development of the ventro-lateral olive during phylogenesis, while the thick line is the connection between the principal and the medial olive.

The fact that, in a caudo-frontal examination, the medial olive becomes thinner, can also be read from the table.

Although we may thus be able to explain the morphological features in a general way, the peculiarities of the olives in the different orders cannot be understood without studying the tracts, in which their reason must be found. So I shall not enter deeper into the question here.

Histology.

I have described the cell-type of the olive in Birds more exactly, because of its being only little known there, whereas we have for Mammals the excellent descriptions of Cajal (Literature, 5—1909) based on silver-preparations. Therefore it would be useless to describe at length the cells stained after v. Gieson, in this class.

Cajal states that the protoplasmatic arborisation of the olive-cells keeps pace with the development of the Mammal in question. This fact is affirmed by Ziehen (1903—1913) and is perfectly accordant with the more complicated structure of the olive in higher Mammals than in lower ones, both being caused by the necessity of receiving more stimuli.

I have only studied the two following histological questions:

1°. do the three parts, which we distinguish in the olivary complex, exhibit constant histological differences?

2°. does the olive-cell form a well-defined type as contrasted with that of other nuclei?

It seems to me that the first question must be answered in the negative. Speaking generally, all three oliveparts have the same histo-

logical structure. The same small oval cells with a distinctly visible nucleus and nucleolus, are situated in the similar granular substance, richly provided with dark coloured glia-nuclei and capillaria. Their differences are even so little, that they form a unit as contrasted with the surrounding nuclei (f. i. nucl. raphes, nucl. lateralis); in such a degree that by a histological research it is possible to ascertain dubious places as belonging to the olfactory-complex. Even the often mentioned out-growth of the dorsal cap, which is indistinct and poorly developed in higher Mammals (*Elephas*, *Anthropopithecus troglodytes*) is recognizable by its histological structure.

Still I will not deny that little quantitative differences in various olive-parts can be found.

Generally the dorsal olive is poorest in cells, but then it is also the part, through which most fibres pass. The cell-accumulation also seems to be less great in the centre of strongly developed olive-parts f. i. in the medial olive of Cetacea and in the dorsal lamella of the principal olive in *Elephas*. This, however, is not on account of the grey substance being transversed by fibre-strands, but because in those large olive-parts the cells are so to say heaped together at the border (perhaps I had better say: on the sur-

face c. f. the similar condition in *Cacatua* — pag. 57). Figure 92 shows this cell-division in *Elephas*, where it is obvious that the cells are most heaped together at the ventro-lateral border of the olive. Sometimes one gets the impression that also the lamellated olive in Primates (f. i. in *Cebus*) is more or less paved with cells. As these lamellae are very thin, however, the fact in question can be less easily ascertained than in the big lamella of *Elephas*.

In studying cell-præparations of many Mammals, one gets the impression, that in the ventro-lateral part of the principal olive, the cells are more numerous and a little larger than in other places. These facts would be quite accordant with the general tendency to enlarge the surface and the hypothesis, that the stimuli, which influence the olfactory system,

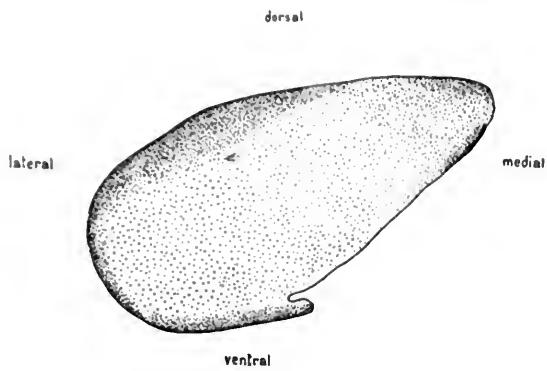


Fig. 92.
Cell-division in the principal olive of
Elephas indicus L

chiefly come from ventro-laterally and that cells with most protoplasm are also most inclined to shift in the direction, from which the majority of stimuli proceeds (neurobiotaxis, Kappers, 1910).

Since stimuli seem at the same time to enlarge the quantity of protoplasm, this may also contribute to the above-mentioned condition.

This histological feature — hitherto unobserved as far as I know — is also found in another sensory nucleus of the nervous system viz.: in the substantia gelatinosa Rolando, of which, according to Cajal (Literature, 5—1909) the larger cells and their dendrites show a tendency to spread along its surface.

Nuclei in the neighbourhood of the olive.

As this is a description of the olive, I shall not describe exactly the nucleus raphes, neither the nucleus lateralis, nor the smaller nuclei in the neighbourhood of the olive. I only mention them because of their lying so near the olive.

Nucleus raphes.

In Macropus, like in Birds, the nucl. raphes appears on about the

same caudal level as the olive, touches it a little higher and still has its full size at the frontal top of the olive.

I found this close contact in no other Mammal¹⁾; more-over the nucleus raphes is developed quite differently: f. i. well-developed in Didelphys, Erinaceus, poorly in Edentata, Oedipomidas, Cebus, Anthropo-

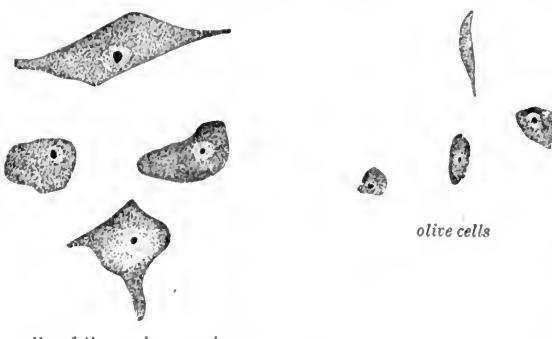


Fig. 93.

Cells of the olive and of the nucleus raphes in
Macropus robustus Gould. — 250 X.

pithecus troglodytes; it is also often situated on a much more frontal level than the olive (f. i. in Talpa, Lepus, Halicore); in some Mammals it lies ventrally of the olive (Macropus, Didelphys, Felis), in others, dorsally of it in the raphe (Erinaceus, Vespertilio).

So in Mammals even the topographical resemblance, with the olive which we found in Birds, is wanting.

The cell-type is also quite different; the olive-cell is relatively small

Note 1: Therefore the nucleus raphes is modelled in Macropus (fig. 69) only.

and oblong, whereas the cells of the nucleus raphe are large reticular elements of multangular form (see fig. 93).

Nucleus lateralis.

I have discussed the nucleus raphe because of its situation quite near the olive. Now there is at the lateral side of the olive a nucleus that has nothing to do with it either: the nucleus lateralis. In Weigert-preparations it is sometimes difficult to distinguish the dorsal olive from that nucleus lateralis¹⁾; cell-stains, however, always show a great difference, as the cells of the nucleus lateralis are, like those of the nucleus raphe, much larger and multangular.

To give an example, I drew the two types as they are found in the Cat (fig. 94).

Small nuclei in the neighbourhood of the olive.

My interpretations of some of those small nuclei is that they belong to the olfactory complex: ventro-lateral outgrowth, medial lamella of the principal olive (vide supra); of the remaining ones we must consider those lateral of the olive, as belonging to the nucleus lateralis.

So only one small nucleus remains to be discussed.

In several Mammals, this nucleus is found between the pyramid and the stratum interolivare, at the lateral point of their border. It is chiefly glious, forming part of a glia-strip which separates the two above-mentioned fibremasses; it does not belong to the olfactory complex, though its cells are more like those of the olive than the reticular elements of the raphe or those of the nucleus lateralis. It is often interrupted in lower Mammals, but present in *Anthropopithecus troglodytes* in many successive sections.

The same nucleus in Man (nucleus conterminalis, Ziehen (1903—1913) is very like that in *Anthropopithecus troglodytes*, only better developed and containing more ganglion-cells. (see Sus, Table 41; Manatus, Table 47; Cebus spec, Table 51; Ateles hybridus, Table 53; *Anthropopithecus troglodytes*, Table 54).



Fig. 94.
Cells of the olive and of the nucleus lateralis in
Felis domestica Brisson. — 250 X.

Note 1: Difficulties may arise because of the nucleus lateralis being often divided into several pieces, which are scattered over the ventro-lateral part of the bulb; so pieces are found ventro-laterally and even ventrally of the inferior olive.

It seems to me incorrect, to homologize this nucleus with the nucleus raphe or with the nucleus arciformis in Man (Kankleit). The nucleus raphe in all Vertebrates is the same typical reticular nucleus, of which the place and cell-type differ widely from the above-mentioned small nucleus and the nucleus arciformis. It is true that the nucleus arciformis reaches the raphe with its pars fissuralis; this is, however, easily explained by the fact, that the nucleus arciformis more or less surrounds the pyramid. Very likely it is best to be interpreted as the most caudal part of the pons, which, one little interruption excepted, passes into the nucleus praecursorius pontis, which again is the direct caudal continuation of the bridge. It has nothing to do with the nucleus raphe of the lower animals, neither with the small glious nucleus described above. This is best to be seen in *Anthropopithecus troglodytes*, in which the nucleus praecursorius pontis (not the nucleus arciformis) is present and at the same time, dorsally of the pyramid, the small glious nucleus.

Embryology.

I examined the ontogenetic development of the olive in Mammals with the help of the excellent collection of embryonic series, belonging to the Laboratory of Anatomy in Amsterdam. I studied series of sections through sheep-embryos of 21,5—22,5—23—23,5—26—27—29—m.M., all measured from skull to rump; and 14,5—15—17—20—23—25—m.M., when the length of the head was measured.

The youngest stage, in which the olive can be found, is represented by the embryo of 21,5 m.M., where only an indistinct medial complex is visible. When examining the higher stages successively, one sees this medial complex becoming more and more distinct, showing very plainly the division into a ventral and a medial component. In still older embryos the medial component shows a cap and a first development of the dorsal olive, which is still connected with the medial complex, is to be seen.

In the next embryo, however, the dorsal olive has become looser, while between it and the medial olive, the principal olive, also connected with the medial one, begins to develop. Only its dorsal lamella is present. The next stage, however, shows both lamellae, of which the dorsal one reaches much farther caudally.

From this stage onward, the principal olive soon becomes better and better developed, while also the other oliveparts take their definitive form.

The Tables 62—65 show the principal lines of this development. In Table 62, only the medial complex is present. The cells migrate from the dorso-lateral somato-sensory area along the lateral border of the bulb to their final place near the raphe (as is easily understood with so purely

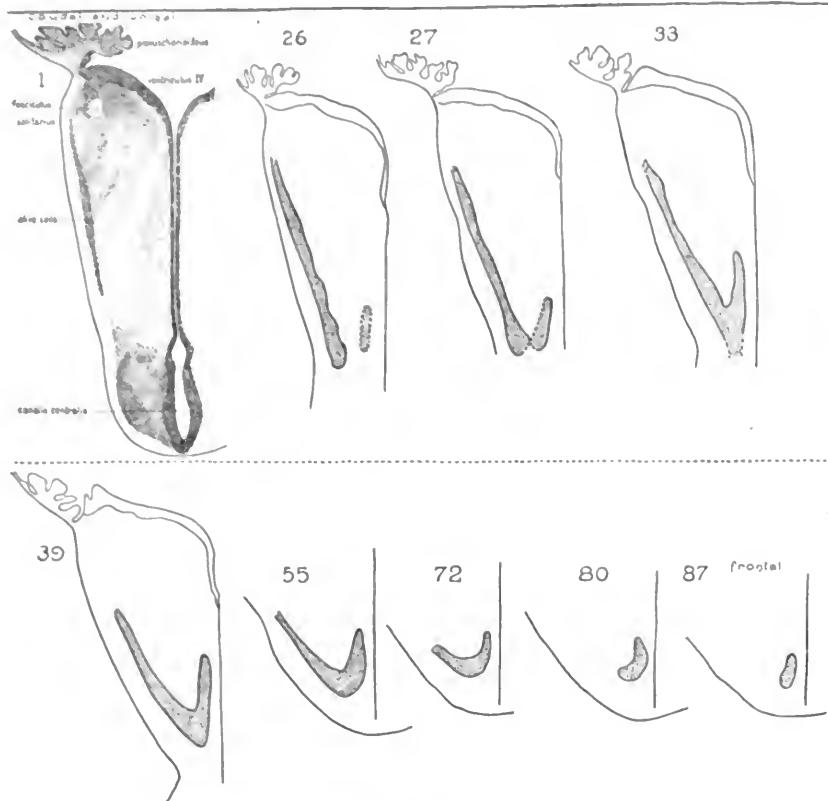


Table 62.
Abbreviated order of sections through the inferior olive of *Ovis aries L.*
Embryo, skull-rump = 23.5 mM.
Size of the section = 10 μ . Magnified 20 \times .

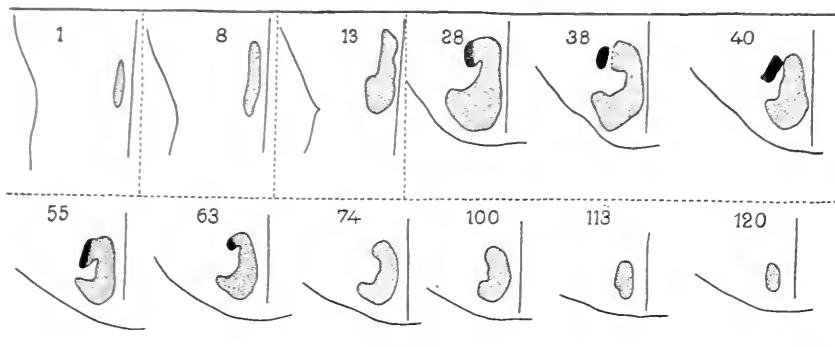


Table 63.
Abbreviated order of sections through the inferior olive of *Ovis aries L.*
Embryo—length of the head 15 mM.—
Size of the section = 10 μ . Magnified 20 \times .

somato-sensory cells as those of the olive and is described for human embryos by Essick (1912).

All embryos I examined, were cut perpendicularly on the maxilla; so the caudal sections through the olive exactly show the bending of the oblongata into the spinal cord ("Nackenbeuge" of His); for that reason the olive is chiefly cut longitudinally and the caudal sections had better be called dorsal. In the next sections also the ventral olive-part appears in view, while most frontally, the olive is cut almost transversally and the common shape of the medial complex can be seen (Table 62, s. 39—87).

Table 63 shows the first development of the dorsal olive. As in this embryo too, the olive is partly cut lengthwise, the dorsal olive takes a more frontal position than might be concluded from the drawings.

In Table 64 we see at the top of the medial olive the same dorso-

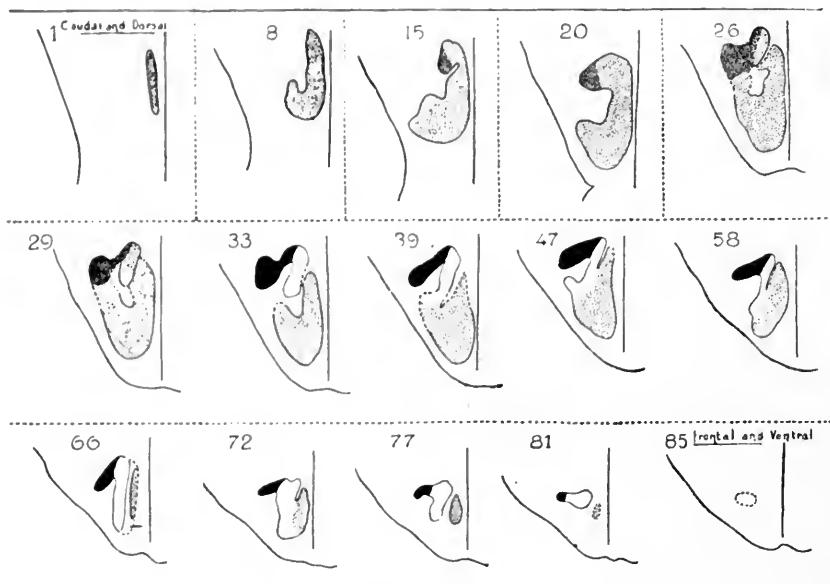


Table 64.

Abbreviated order of sections through the inferior olive of *Ovis aries L.*

Embryo—length of the head 17 mM.—

Size of the section = 10 μ .

Magnified 20 \times .

lateral outgrowth, interpreted in the former Table as dorsal olive; in more frontal sections, also a ventro-lateral outgrowth appears (Table 64, s. 29 etc.) between the dorsal and the medial olive, which is only free from the latter at its frontal top (Table 64, s. 77—85).

The dorsal olive bends into this outgrowth, as it often did into the dorsal lamella of the principal olive, as described in the phylogenetic part of my researches.

Table 65 affirms that it is indeed the dorsal lamella, for till a rather frontal level, we see quite the same here as in the younger stages,

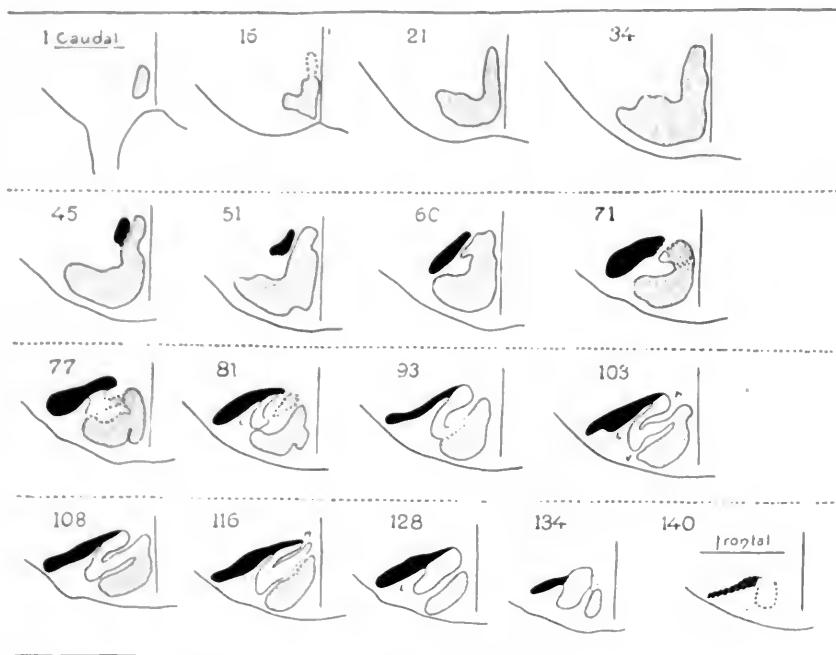


Table 65.

Abbreviated order of sections through the inferior olive of *Ovis aries L.*

Embryo-length of the head 20 mM.—

Size of the section = 10 μ .

Magnified 20 \times .

but on that level, also the medial lamella becomes independent from the medial complex, so that a medial hilus appears and the „vierblätter-form” of the adult specimen is visible. Like the dorsal lamella in former stages, the principal olive, connected with the dorsal one, reaches more frontally than the medial olive.

Conclusions:

So we find in the embryology, what we saw in the phylogenetic development:

The medial complex is present first, and remains alone for a rather

long time; then the dorsal olive and soon also the principal olive appear, both connected with the medial complex and becoming independent during their further development.

The principal olive chiefly grows in a caudal direction, though also frontad, and, as it develops ventro-laterally, its lateral lamella first appears and reaches most caudally.

CHAPTER IV.

The olive of Mammals, Echidna and Birds compared with each other.

After having described the olive in Mammals, I once more return to that of Birds and of Echidna.

Speaking generally, we have found in Mammals three parts, situated:

Ventro-medially (medial olive),

Dorso-laterally (dorsal olive) and

Ventro-laterally (ventro-lateral or principal olive).

Also in Birds we found the cells of the olfactory complex chiefly accumulated at these three places:

Ventro-medially (medial part of the dorsal lamella),

Dorso-laterally (lateral part of the dorsal lamella) and

Ventro-laterally (distinct lateral part of the ventral lamella).

But then the ventro-medial and the dorso-lateral accumulation are connected (dorsal lamella).

Now the olive of Echidna, the most primitive Mammal, also shows a connection of the medial and the lateral part into one lamella, which encloses the ventral part. In Echidna, however, this lamella is arched, its two parts being placed in a plane more parallel to the raphe, as is the case with all Mammals.

When we imagine the avian olfactory lamellae placed in a similar plane and not stretching laterally along the border of the bulb, we get a complex very like that of Echidna.

The many points of resemblance between the three groups:

Monotremata, other Mammals and Birds, are in short these:

Birds.	Echidna.	Mammals.
1°. cell-accumulation:	1°.	1°.
a. medial	the same	the same
b. dorso-lateral	the same	the same
c. ventro-lateral	ventral	ventro-lateral,
2°. medial and dorso-lateral part always connected into one lamella.	2°. the same	2°. medial and dorsal part generally separated, but often united in caudal sections and embryonically.
3°. the medial part shows a cap.	3°. no cap could be ascertained	3°. the medial part shows a cap.
4°. the dorso-lateral part is flat (more than a and c).	4°. the same	4°. the same.
5°. the dorso-lateral part reaches most caudally.	5°. the same	5°. the medial part reaches most caudally (or the medial and the dorsal one together).
6°. the dorso-lateral part reaches most laterally in the middle of the olive-length.	6°. the same	6°. the same.
7°. the ventro-lateral part is chiefly present or most distinct on a frontal level, especially in <i>Casuaris</i> .	7°. the same	7°. the same, especially in lowest Mammals.
8°. of the three parts, the ventro-lateral one differs most in the various Birds (youngest olivepart?). ¹⁾	8°. only one specimen was examined.	8°. the same as in Birds.
9°. the ventro-lateral part is connected with the medial one on a frontal level.	9°. the same	9°. entirely connected in the very low Mammals; otherwise it is connected with the medial olive on a caudal level only.

Now, though there are differences (as may be expected with so different groups of animals), the resemblances are yet so striking, that it is not too bold to suppose the possibility of an analogy between the three above-mentioned parts in Birds and Mammals.

Note 1: I examined various stages of the ontogenetic development of the olive in *Gallus gallus* (L.), and found that both lamellae appeared at about the same time.

CHAPTER V.

The inferior olive in Man.

I do not intend to describe the human olive in extenso, as its anatomy has been known for a long time.

As, however, the knowledge of the olivary phylogenesis enables us, better to understand the general form as well as the peculiarities of the olive in Man, a short discussion of the latter had best be placed here.

I also studied the ontogenetic development in a series of human embryos which measured from head to rump:

27—35—44—
55—65—74 m.M.;
14—28—35—
42—50 c.M. (newborn baby).

I further examined two children (of 5 and 8 months) and several adult specimens.

Waxreconstructions were made of the olives of embryos measuring:

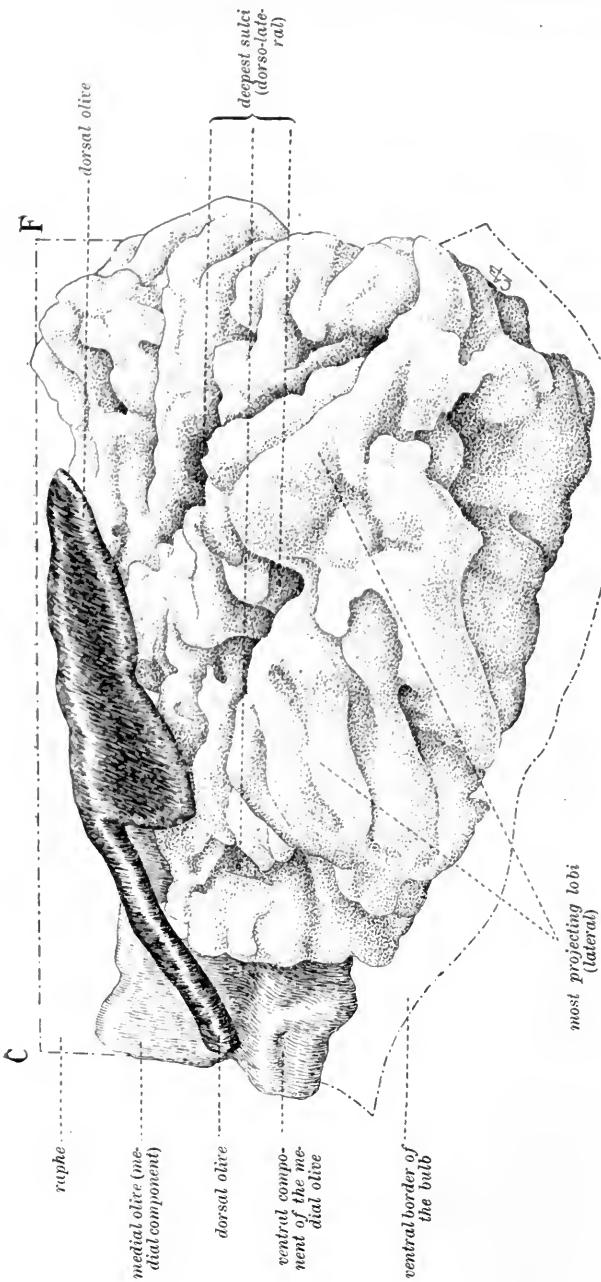


Fig. 95.
Inferior olive of an adult man. — 9 X (lateral view).

27 m.M.; 14—28—50—e.M.; of a 5 month-old child and of an adult¹⁾. At the same time, I composed Tables, showing an abbreviated order of sections through the olives of the specimens of the following sizes:

27—35—55—74 m.M.;
14—28 e.M.; of the 5 month-old child and of an adult.

In the series of mammalian olives, the human olive represents the highest stage.

Though very like that in *Anthropopithecus troglodytes*, the ventro-lateral (principal) olive in Man is still more prominent by its enormous extension as well ventro-laterally as caudally and, though in a less degree, also frontally.

Studying the waxreconstructions of the olive in Man (fig. 95) and Child (figs. 96, 97), and the Tables 66 and 67, one sees that:

The medial olive shows the two components, of which the medial one reaches most caudally.

In these caudal sections, it is difficult to distinguish the medial olive from the rest of the cornu anterius (Table 66, sections 1 and 3: the olive is indicated by fine dots, the

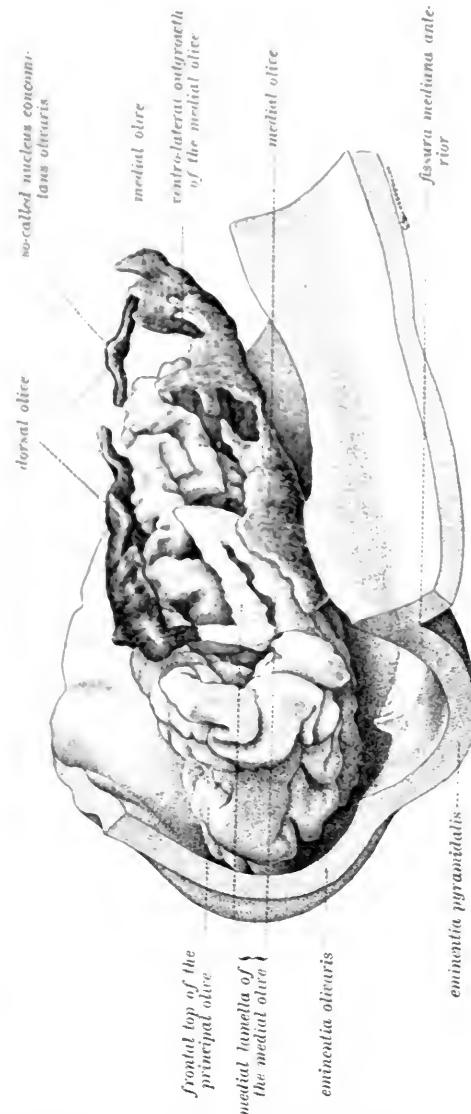


Fig. 96.
Inferior olive of a child, old 5 months, ± 9 × (fronto-medial view).

anterior horn by double-crosshatching, see also Ziehen (Literature, 34, p. 46 — 1903—1913).

Note 1: This last waxreconstruction was made in the Institute before I started my researches on the Inferior olive.

For the greater part, however, these cells belong to the medial olive; in embryos, they can easily be distinguished from those of the anterior horn, and also here, the medial component is clearly the most caudal part. In a few sections, the ventral component shows the ventral groove, which we have so often seen in the various Mammals (Table 66, s. 13; Table 67, s. 14).

More frontally a dorsal cap with a ventro-lateral outgrowth is visible, at about the caudal pole of the principal olive. No further explication is needed, as we know it so well by our phylogenetic examination (Table 66, s. 25, 29; Table 67, s. 24).

When, more frontally, the cap too has disappeared, the medial olive is very small in some sections, like in *Elephas*, *Cebus fatuellus*, *Ateles*, *Anthropopithecus troglodytes*.

In the next sections we see it increase once more, while at its ventral side a small nucleus appears, which for the greater part contains gliacells. *Ziehen* called it: „nucleus conterminalis”, while he gave the name of „repagulum” to a similar glioous nucleus, situated along the medial side of the medial olive, and, more frontally, of the medial lamella of the principal olive (Table 66, s. 47 etc.; Table 67, s. 28, 32 etc.).

Continuing our examination in a frontal direction, we see a strand of olfactory cells appear along the lateral side of the medial olive (Table 66, s. 68 a. s. o. and Table 67, s. 72 etc.), which now, knowing the olive of *Ateles* and *Anthropopithecus troglodytes*, we can easily interprete as the medial lamella of the principal olive (*Ziehen*: nucleus parolivaris medialis intermedius). My study of the ontogenesis has quite affirmed this interpretation.

It would be superfluous to state, that neither repagulum nor nucl. conterminalis, have anything to do with the olfactory complex. If they did not often lie so very near it, they would not even be mentioned in this study. The medial olive disappears rather far below the frontal top of the principal olive.

The *dorsal olive*, and especially its caudal part, is not so easily interpreted. This olive-part probably appears very caudally (Table 66, s. 7), having about the same position as in other Primates¹⁾ (*Anthropopithecus troglodytes*); more frontally the principal olive separates the medial and the dorsal olive, so that the latter takes a more dorsal position. Between the dorsal olive and the cap of the medial olive, a small nucleus appears, which can only be interpreted by studying the ontogenesis. In the human embryo of 74 mM. (Table 71, sections 46—57), we see the same small

Note 1: Just as in higher Primates the dorsal olive in Man is most times divided into a caudal and a frontal part; the caudal part is the nucleus concomitans olivaris *Ziehen*.

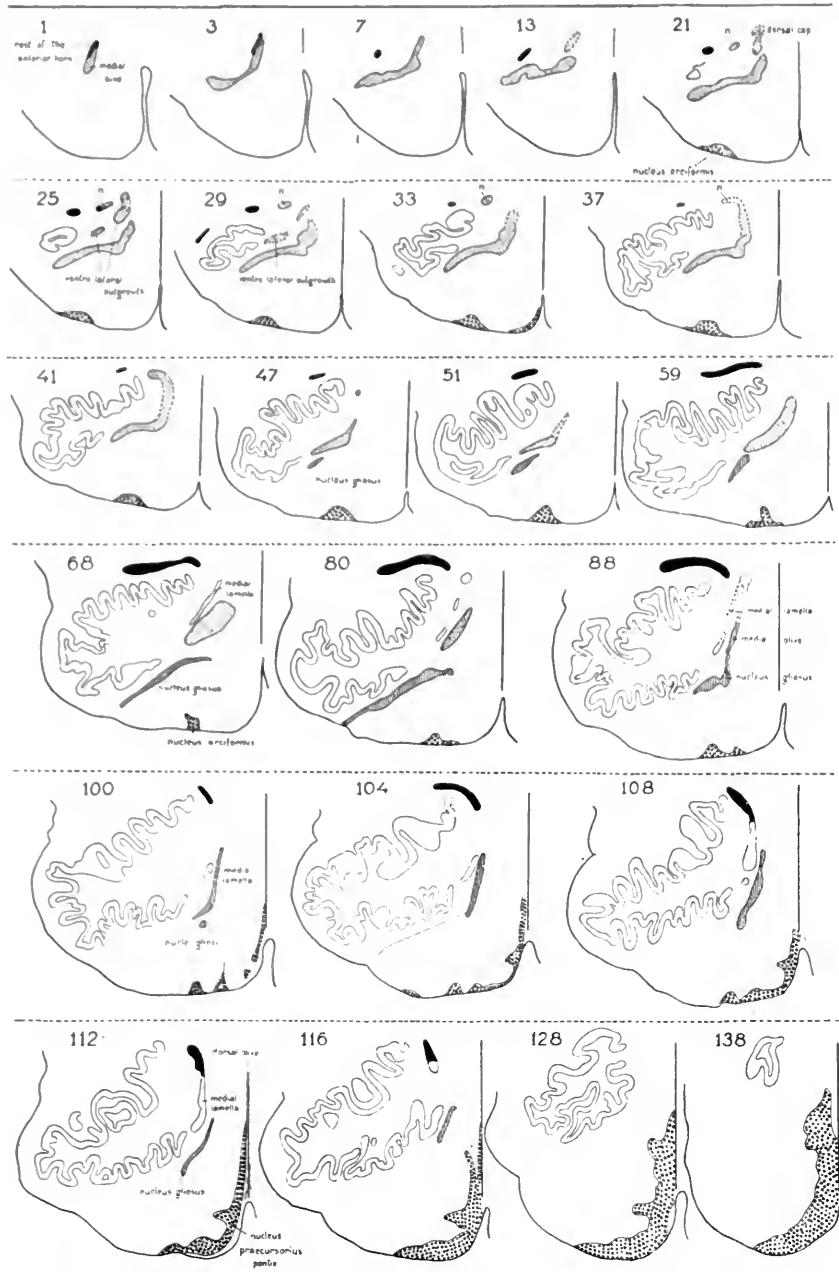


Table 66.

Abbreviated order of sections through the inferior olive of *Homo (adultus)*.

Size of the section = $3 \times (20-40 \mu)$. Magnified $\pm 4 \times$.

nucleus (indicated by η), but here it is as well connected with the dorsal olive, as with the cap of the medial one; of this connection only that with the cap remains a little more frontally.

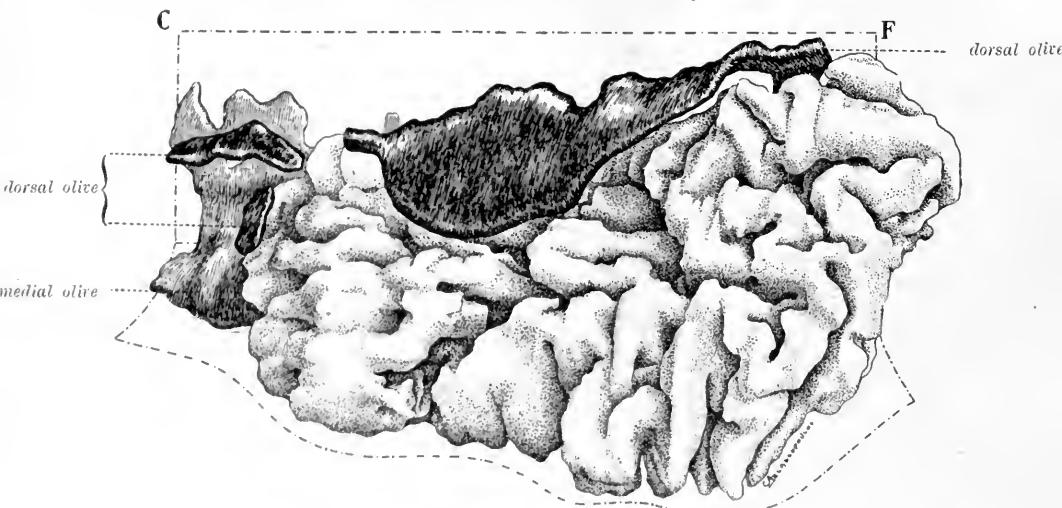


Fig. 97.

The same olive (as in fig. 96), taken out of the bulb. — 9.5 × (lateral view).

The same can be observed in the embryo of 14 cM. (Table 72), only here the small nucleus has become independent from the dorsal olive.

From this stage onward, the nucleus in question keeps about the same form and size.

Very likely it is a centre of growth¹⁾, as the dorsal olive and the ventro-lateral one are both connected with the cap; when these olive-parts have become independent, the place of connection remains as a small separate nucleus.

Like in Ateles and in *Anthropopithecus troglodytes*, the dorsal olive increases more frontally, when the principal olive enlarges.

Most frontally, it bends ventralward round the top of the dorsal lamella and becomes connected with (or approaches) the free part of the medial lamella (Table 66, s. 108—116; Table 67, s. 111—118).

Although it disappears caudally of the frontal top of the principal olive, it reaches more frontally than the medial one (like in all Mammals).

In its main features, *the principal olive*, of which the sulci and gyri will afterwards be discussed, presents the same structure as in Anthro-

Note 1: In embryos, the small nucleus in question is indeed like a matrix of olfactory cells, containing many darkly stained cellbodies, exactly like the medial olive in youngest stages.

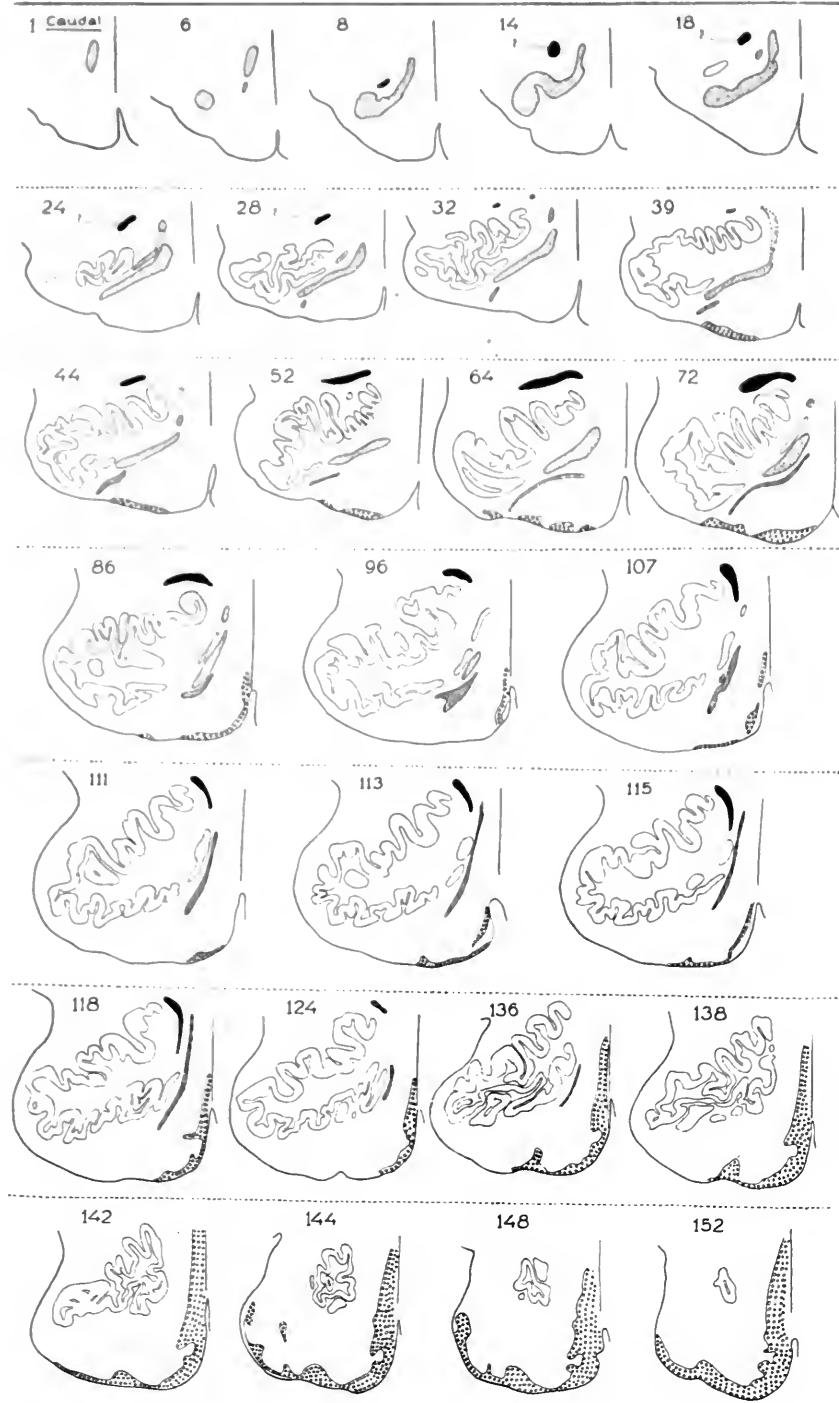


Table 67.

Abbreviated order of sections through the inferior olive of a child (5 months old).
Size of the section = $\pm 80 \mu$. Magnified $\pm 4 \times$.

popithecus troglodytes; it covers about 85—86 % of the length of the total olfactory complex. Though closed at its ends, the principal olive shows over the whole distance a distinct medial hilus, formed by the two well-known lamellae, of which the dorsal one is the most important.

Only on a frontal level, the medial lamella too becomes long, but this prolongation has become an almost independent nucleus, like in *Anthropopithecus troglodytes*. It is sometimes connected with the ventral part of the medial lamella (five month-old child, fig. 96), sometimes with the dorsal olive (fig. 96, Table 66, s. 108 etc.)¹.

That it is indeed the medial lamella, is also affirmed by the ontogenesis. In the embryo of 74 m.M., we still find the same condition as in lower Mammals, in which the medial lamella bends ventrally into the medial olive (Table 71, s. 100 etc.); in the embryo of 14 cM., the medial lamella has already become thinner (Table 72, s. 48—68), while in that of 28 cM., it is the free thin strip of grey substance (Table 73, s. 58—87), which we see in the adult specimen.

A few words remain to be said about the nuclei in the neighbourhood of the olive.

I have already described *the nucleus lateralis* and I have nothing to add to it. In Man too, a study of the cells can prevent a confusion with the dorsal olive.

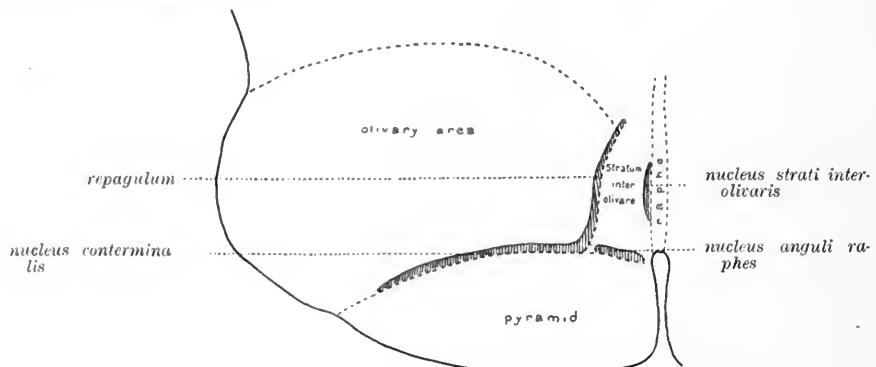


Fig. 98.

Schematical drawing, showing the position of the various glious nuclei.

The nucleus raphes lies too dorsally to be confounded with the olfactory complex; moreover its celltype is totally different.

The nucleus arciformis (which is indicated in the table by little circles, just like *the nucl. praecursorius pontis*, because of their gradual

Note 1: Nucleus parolivaris medialis intermedius Ziehen.

transition and their belonging together ontogenetically), has nothing to do with the small glious nuclei, ventral and medial of the olfactory com-

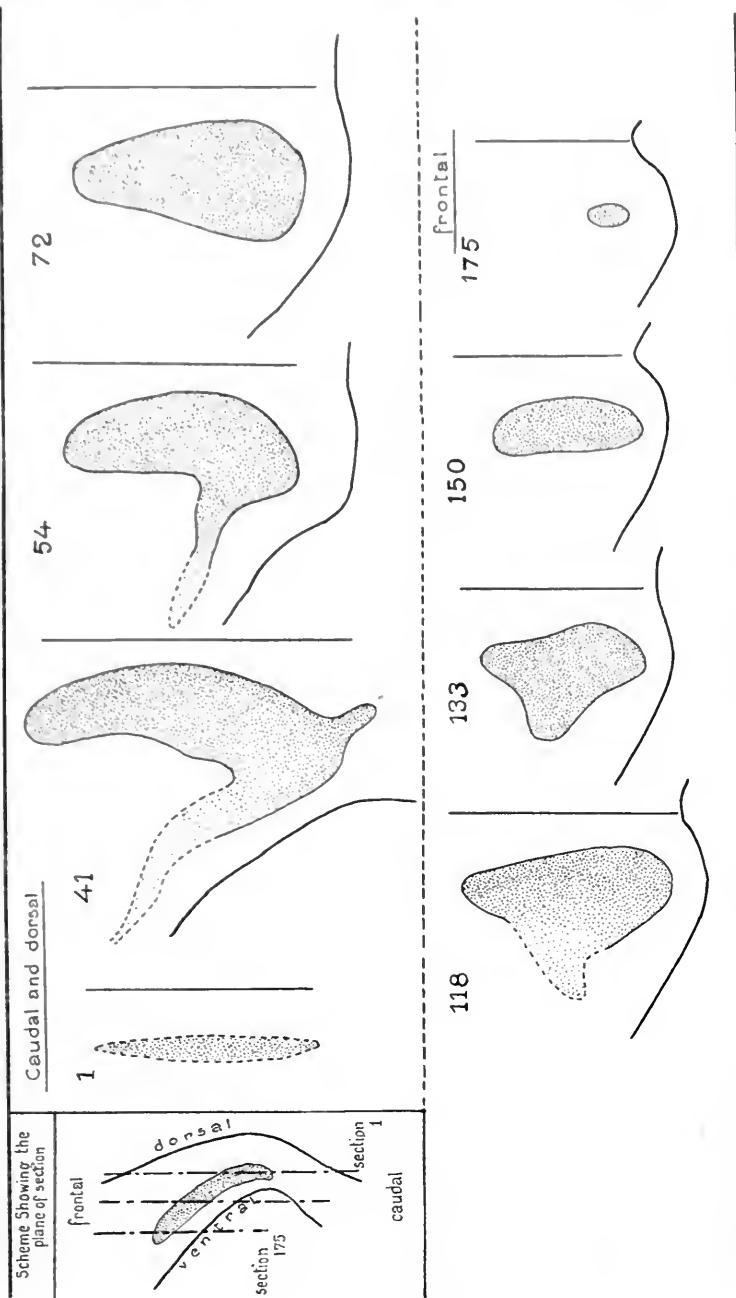


Table 68.
Abbreviated order of sections through the inferior olive of *E. humanum* 27 mm.
Magnified 35 X.

plex, as has already been mentioned in the discussion of *Anthropopithecus troglodytes*.

Of these small nuclei, those that lie quite near the medial olive are the most constant; Ziehen (34) called them "nucleus conterminalis" (ventral of the medial olive in caudal regions) and "repagulum" (medial of the medial olive more frontally). Moreover he described a "nucleus anguli raphes", situated in the prolongation of the "nucleus conterminalis", and a "nucleus strati interolivaris" quite near the raphe. It seems to me superfluous to give separate names to all these nuclei. They hardly deserve the name of "nucleus", as they are for the greater part glious; indeed they seem to be nothing else than accumulations of a few cells in the glious septa between the fibre-areas of this region. In fig. 98 their position is represented schematically; it can be seen that they are situated exactly between the pyramid, the olfactory complex and the stratum interolivare.

I have simply called them glious nuclei, without pretending to give them a new name, and I have only described them because of their position so near the olive and because confusions might arise (Kankeleit), especially in lower Mammals.

Summarizing, I distinguish the following separate groups of nuclei in the region of the olive:

- 1° *Olfactory complex* — in which I also include the nucleus concormitans olivaris (= dorsal olive) and the nucleus parolivaris medialis intermedius (= medial lamella of the principal olive)
- 2° *Nucleus lateralis*
- 3° *Nucleus raphe*
- 4° *Nuclei gliosi*
- 5° *Nucleus arciformis, nucleus praecursorius pontis.*

Embryology.

The embryology of the Mammalian olive has already for the greater part been described in my discussion of the ontogenetic development of the sheep, while several points of the human olive-ontogenesis have also been mentioned. Therefore, I will here only discuss in short the ontogenetic development of the olive in Man.

In the embryo of 27 m.M., we only see the medial complex (Table 68; the olive was nowhere cut quite transversely, on caudal levels even nearly longitudinally; I added to the drawings a scheme, showing the plane of section through the olive).

Caudally, (Table 68, s. 41 and 54) we see a lateral outgrowth, partly corresponding to the cells, described by Essick (1912), which shift along the lateral border of the bulb, originating from the somato-sensory area,

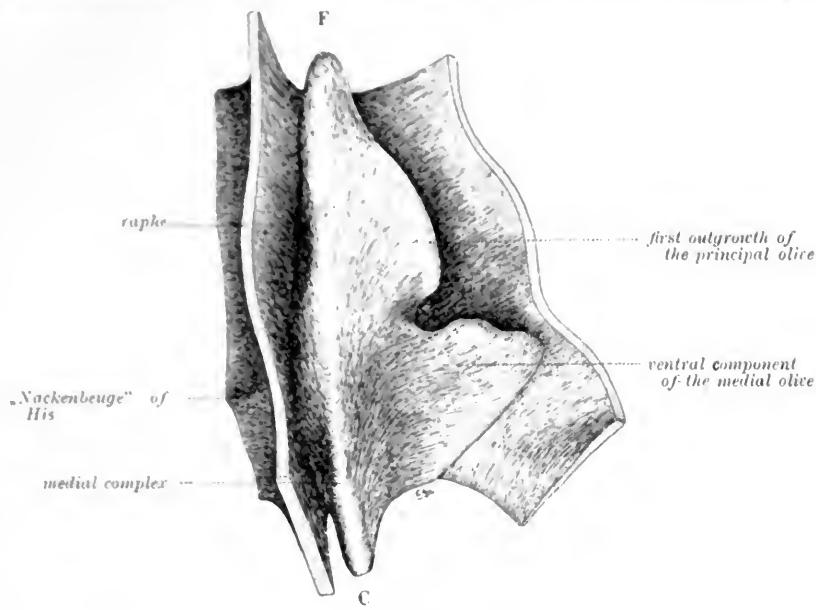


Fig. 99.

Inferior olive of a *human embryo* of 27 m.M. — 37.5 X (dorsal view).

partly, however, being perhaps the ventral component of the medial olive, which supposition is affirmed by the next embryo (35 m.M., Table 69, s. 23).

Much more frontally we again find a lateral outgrowth, which is the beginning of the principal olive, growing out ventro-laterally and caudally. Both lateral projections are well visible in the waxreconstruction (fig. 99).

Table 69, representing an abbreviated order of sections through the olive of *an embryo* of 35 m.M., distinctly shows the ventral component (s. 23), while more frontally, once more a lateral outgrowth appears, this time doubtless the principal olive, with the two lamellae and a medial hilus.

The medial lamella is hardly visible, whereas the lateral one is very well-developed. The olive is cut nearly longitudinally, as is shown by the scheme in the Table. In the frontal half, the dorsal olive is present, but poorly developed and often very indistinct.

While the embryology partly repeats the phylogenesis (medial complex), it also shows the later form of the adult specimen, for in the embryo

Scheme, Showing the
plane of section

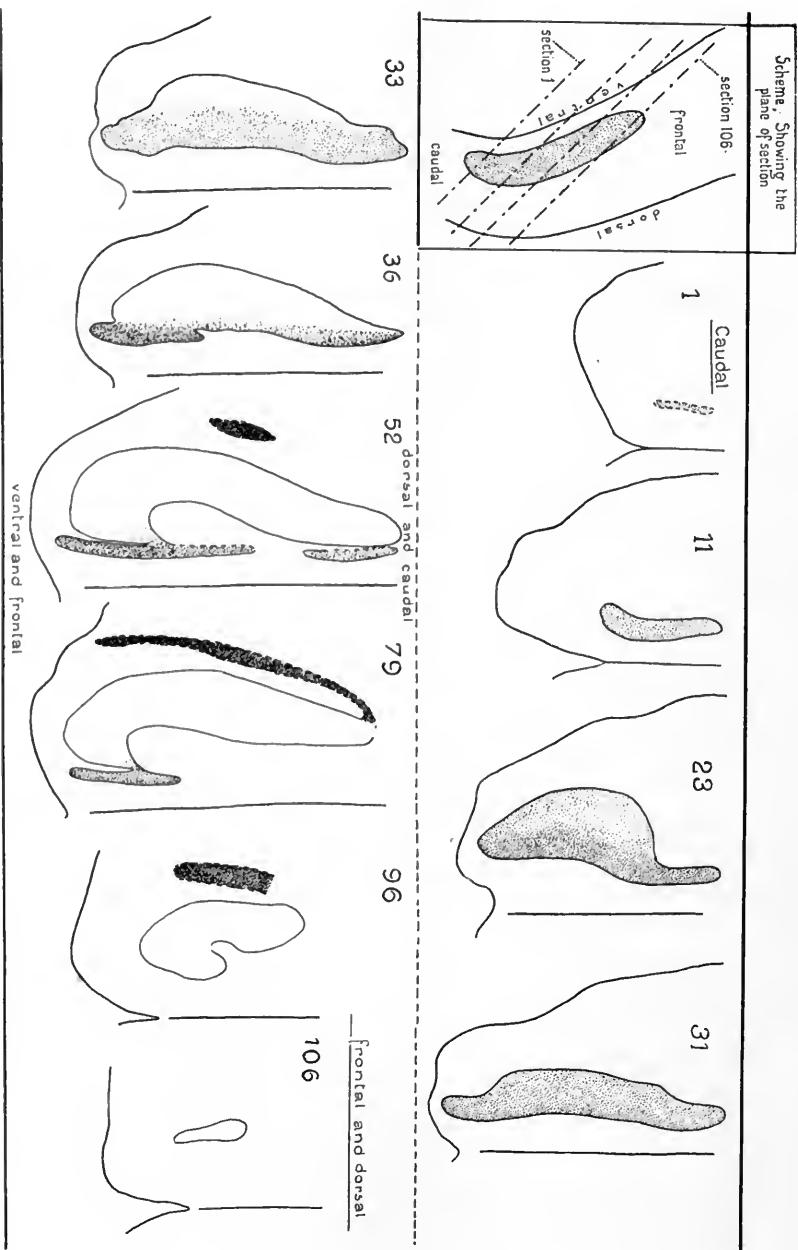


Table 69.

Abbreviated order of sections through the inferior olive of *Embryo humanum* 35 mM.
Size of the section = 125 μ . Magnified 30 X.

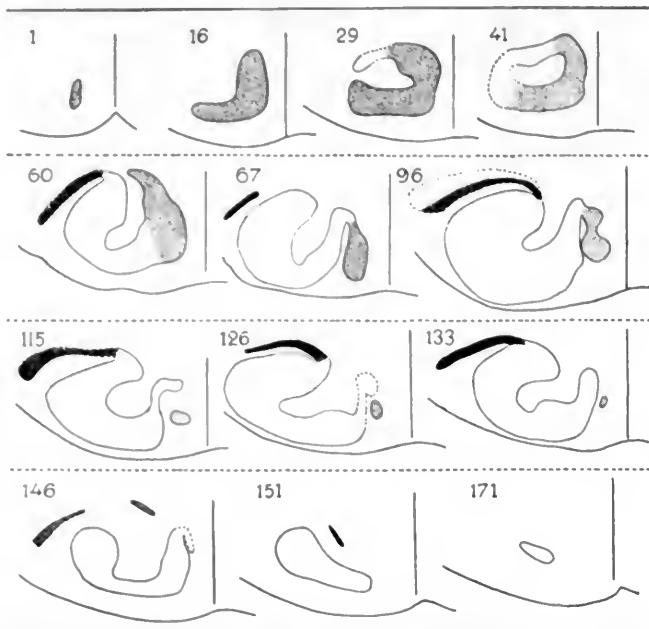


Table 70.
Abbreviated order of sections through the inferior olive of
Embryo humanum 55 mM.
Magnified 20 X.

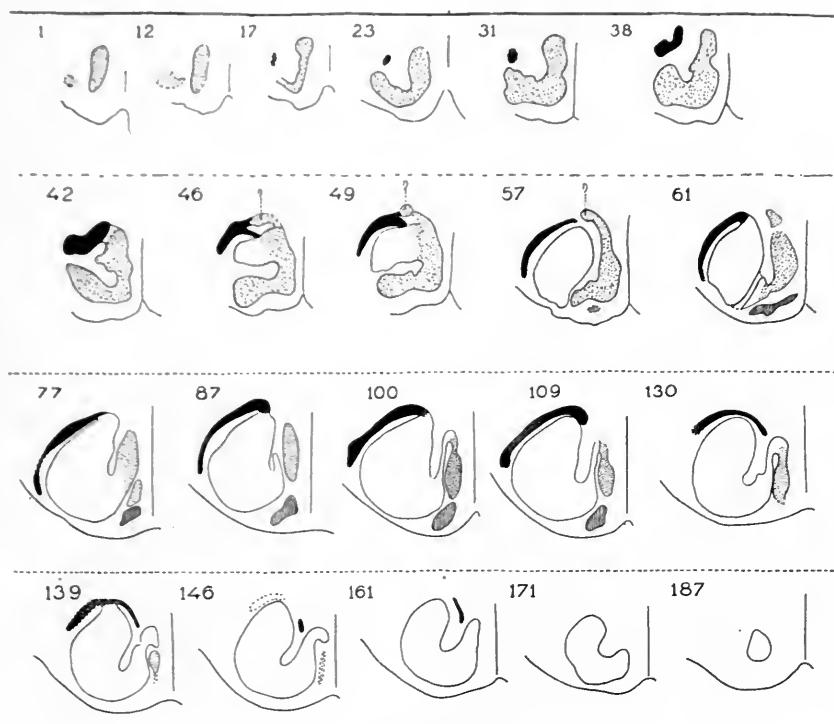


Table 71.
Abbreviated order of sections through the inferior olive of *Embryo humanum* 74 mM.
Magnified 20 X.

of 35 m.M., the principal olive is already the most important part, and well-developed before the dorsal one.

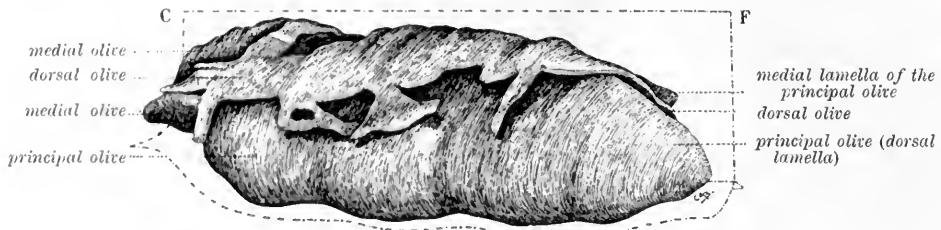


Fig. 100.

Inferior olive of a human embryo of 14 cM. — 18 X. (lateral view).

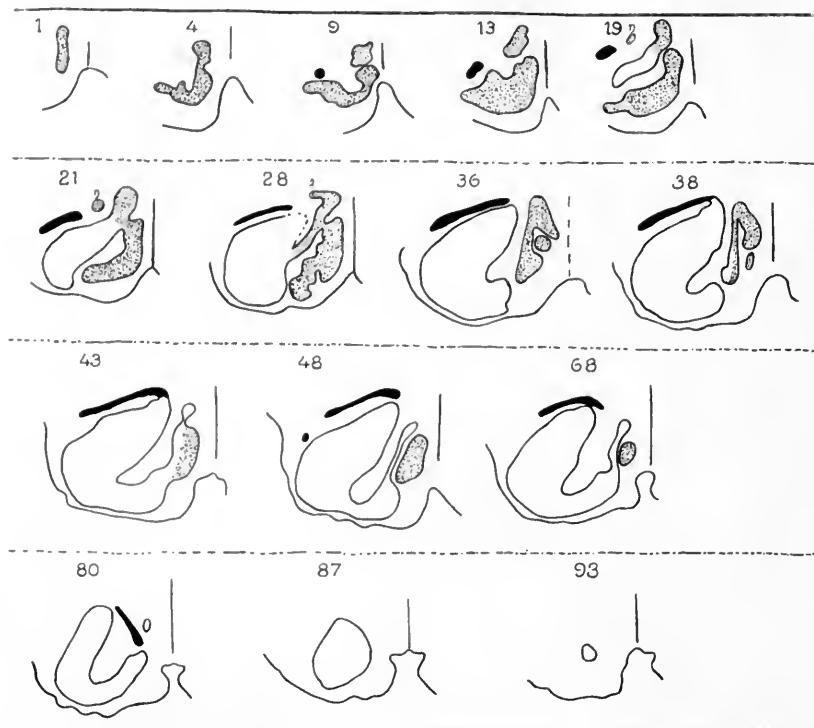


Table 72.

Abbreviated order of sections through the inferior olive of *Embryo humanum* 14 cM.
Size of the section = 50 μ . Magnified 20 X.

From this stage onward, the principal olive develops rapidly.

In the embryo of 55 m.M. (Table 70), also the medial lamella is well-developed in frontal levels. The dorsal olive, however, is still indistinct, its presence cannot even be ascertained in caudal regions.

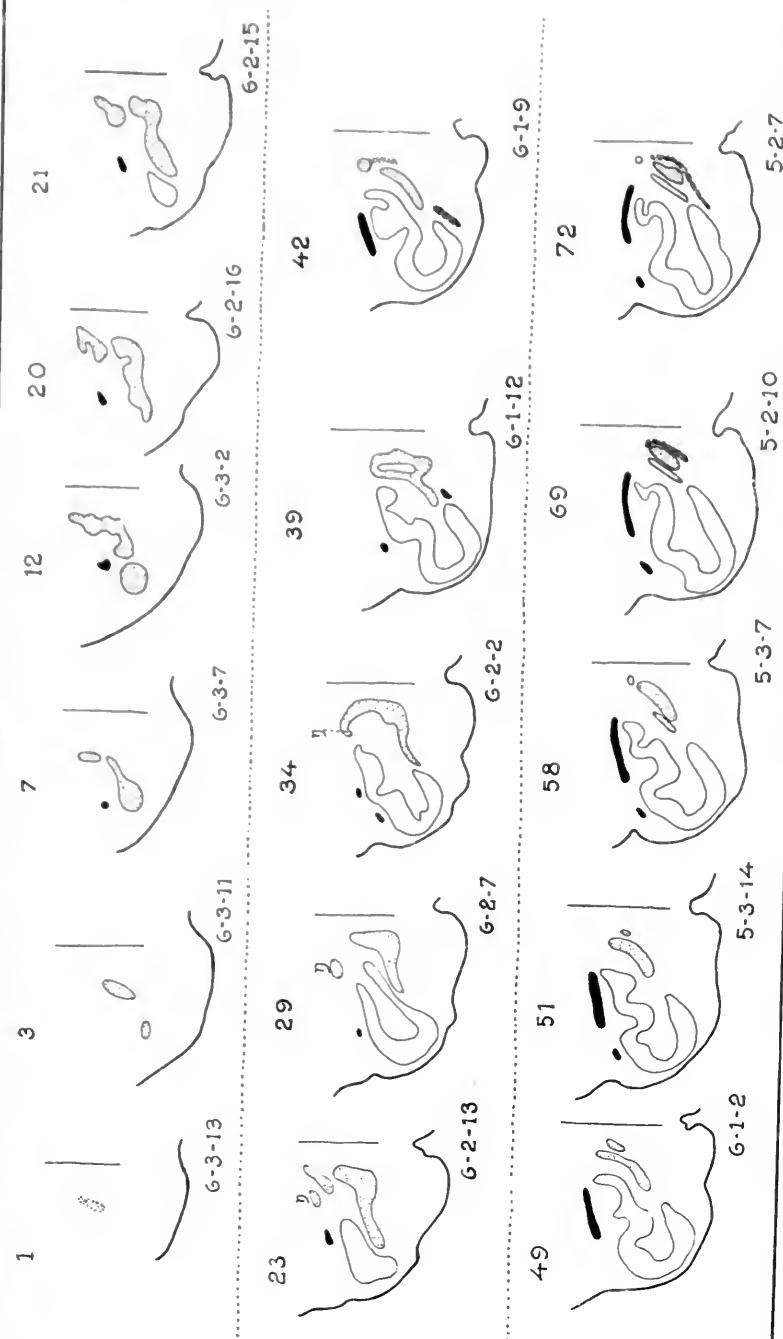


Table 73.
Abbreviated order of sections through the inferior olive of *Embryo humanum* 28 cm.
Size of the section = 50 μ .
Magnified $\pm 10 \times$.

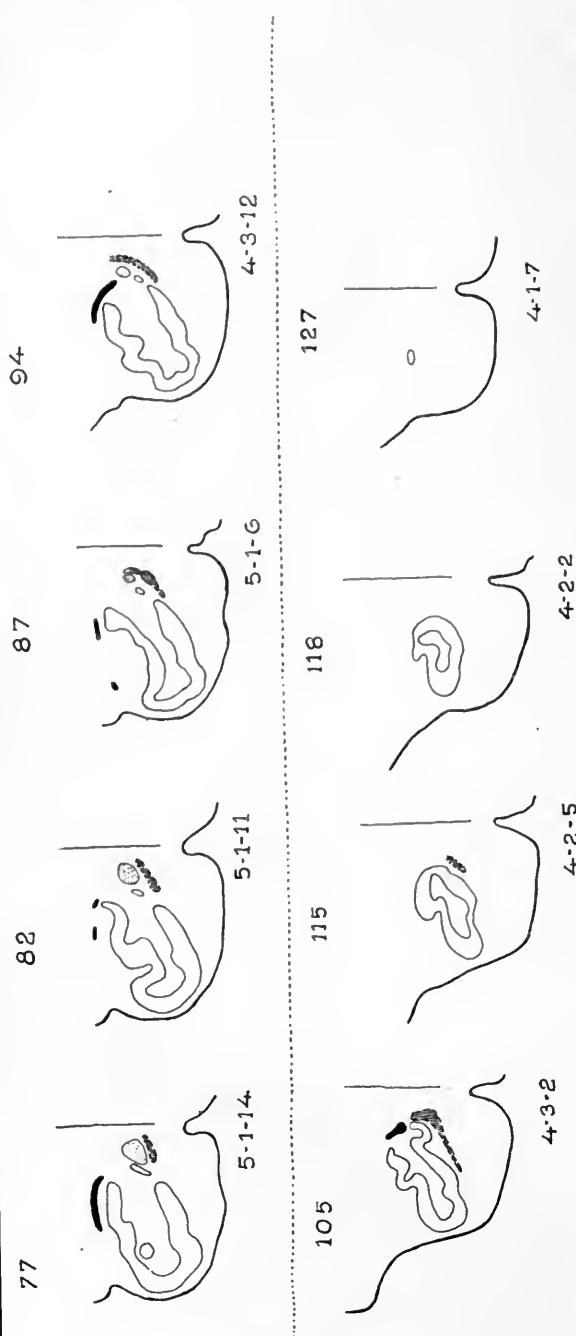


Table 73bis.

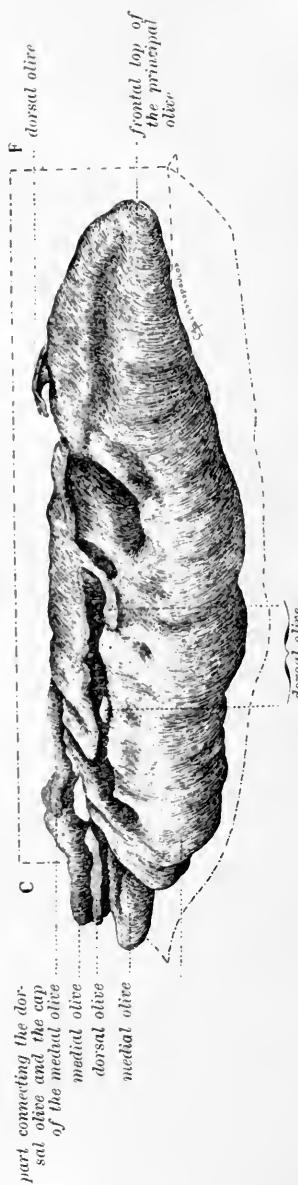


Fig. 401.

In the next stages (65 and 74 m.M.), however, it is much more distinct and has the form of the dorsal olive in adult specimens (Table 71).

I have already discussed its connection with the cap of the medial olive when I explained the significance of the small nucleus. (pag. 146).

The olives of the following embryos (of 14 and 28 c.M.), were modelled (figs. 100 and 101, Tables 72 and 73).

The accessory olives have about the definitive form, only the principal olive is still growing.

The following percentages show how much of the total olive-length is occupied by the principal olive in the various stages of ontogenetic development.

Embryo of 55 m.M.	about 62%
Embryo of 74 m.M.	about 71%
Embryo of 14 c.M.	about 78%
Embryo of 28 c.M.	about 84%
Five month-old child	85—86%
Adult	85—86%

So, as will be seen, from about 28 c.M. (sixth month) onward, it does not grow much further caudally (that is, when compared with the medial olive, for of course the whole complex continues growing), but chiefly develops laterally, becoming more and more lamellated.

Gyri and Sulci.

The principal olive of the human embryo of 14 c.M. does not yet have any sulcus; in that of the next stage (28 c.M.), we see one longitudinal dorso-lateral sulcus, which is, however, interrupted, like in Ateles, by a bridge between the two convolutions (Table 73, fig. 101).

The next embryos I studied (35 and 42 c.M.) already showed a fully lamellated principal olive: like in lower Primates, the lateral lamella, which is much better developed than the medial one, shows the most and the deepest sulci. The many smaller lobes, which arise in the depth of the sulci, divide the latter and disperse them; in this way they merge into other, equally dispersed sulci, thus forming lines, which are no longer longitudinal. Though the sulci of the principal olive in the new-born infant are rather complicated, their longitudinal type can still be recognised.

The medial lamella shows sulci which are much more regular, but these too, become more twisted as the olive extends laterally.

As has been mentioned above, from about the end of the sixth month, the olive does not grow caudally any longer, but enlarges only ventro-laterally; in consequence of this, its longitudinal dimension does no

longer predominate to such an extent, while its lamellae become more and more folded.

Miss Florence R. Sabin (1901) reconstructed the olive of a newborn infant. She divides the olive into four lobi, separated by sulci, which are more or less directed dorso-ventrally, and are most clearly visible on the lateral surface of the olive.

Lewis H. Weed (1914) also made a very valuable wax-model of the olive of an adult Man, by which the general features, communicated by Miss Sabin, were affirmed.

From a purely descriptive point of view, my results are perfectly accordant with those of Miss Sabin and of Weed. In the same way as the olive-model of Weed differed in some points from Miss Sabin's reconstruction, my models partly differ from both olives of the two above-mentioned authors. This affirms the opinion, I formed in studying several olives of adult Men, that they are similar in a general sense, but that little differences do occur.

That I do not describe at length the sulci and gyri of my own models and that I do not dwell any longer on the anatomical descriptions of Miss Sabin and Weed, finds its reason in the character of this study, which is a phylogenetic and ontogenetic research.

For, as a matter of course, the division of the olive in lobes and the description of its sulci by these authors can only have a descriptive significance, as both examined one specimen only.

Surely the sulci, first mentioned by Miss Sabin, are not phylogenetic or ontogenetic unities, as they have originated by the confusing of two or more other grooves.

We distinctly see, that the grooves are still deepest on the dorso-lateral surface and that the principal lobi are still directed ventro-laterally and chiefly laterally (fig. 95). So, if we wish to know why the olive, situated medially in Fishes (which is not astonishing in primitive animals) grows out in Birds and Mammals, we must look for the reason in a lateral source of stimuli which increases during the phylogenesis. This also makes us understand the enormous development of the principal olive, and the arrangement of its sulci.

CHAPTER VI.

General conclusions.

So, comparing the inferior olives of Fishes, Birds and Mammals, one can see this line in the phylogenetic development:

In lowest Vertebrates (Fishes) only the medial complex, situated near the raphe, is present; in higher animals (Birds, lower Mammals), however, two outgrowths occur, directed dorso-laterally and ventro-laterally.

For some reason or other, the ventro-lateral component of the olfactory complex is then obliged to increase and when it develops more and more, the dorso-lateral one (dorsal olive) is confined to its medial part¹⁾. Also the ventral component of the medial olive is replaced by the new, large, ventro-lateral (principal) olive.

This is confirmed by the study of the ontogenetic development, which follows a similar line.

So by phylogenetic and ontogenetic study we have followed the development of the inferior olive and saw how its ventro-lateral component grew, till in highest Primates it was the dominating part of the olfactory complex.

But why does this part increase so enormously?

Note 1: This is probably the reason why the caudal part of the dorsal olive nearly disappears in Primates; this part, which had a ventral position, is now replaced by the large principal olive, reaching far caudally.

The examples of parts, which decrease, when others develop in the same direction, are manifold, e. f. the medial olive being confined to its medial part at the appearance of the principal olive; in Birds the lateral part of the dorsal lamella takes a much more medial position, when the lateral part of the ventral lamella becomes distinct.

This may be caused by a higher differentiation of motility. Probably various sensory stimuli, having to do with the statics of body and limbs, are correlated in the olive, from where they are conducted to the cerebellum.

Thus can be understood why animals with little motility as Amphiibia and Reptilia, have little or no olive and why it is found so considerably developed in swimming, in flying and in going animals.

So may be explained why Cetacea¹⁾, moving in the same manner as Fishes, have a so enormously developed medial olive (and most striking is, that especially its medial component is hypertrophied).

Similarly it may be, that the hypertrophy of the principal olive in the superior Primates and especially in Man, has to do with the finer differentiation of the movements of the limbs, each of which acquire a greater independency of their motile possibilities.

But a more definite idea of the part, which the olive plays in this static-system, or a supposition of the exact function of its various parts, seems to me quite impossible, without an exact knowledge of the tracts (the afferent ones) or without experimental research.

Note 1: The other aquatic Mammals cannot be considered for a comparision of their movements with those of Fishes and Dolphins.

Post scriptum.

I will not end this paper without mentioning the publications by Holmes and Stewart (1908) and those by Brouwer (1913 and 1915).

For these researches do not only clearly show an analogy between the phylogenesis of the cerebellum and that of the olive, but they form a valuable affirmation of my own results.

From the researches by Holmes and Stewart it appears that:

1°. if a lesion of the cerebellum was limited to the lateral lobes of this organ, the medial accessory olives were intact, whereas:

2°. they were changed, when the vermis had also degenerated.

Brouwer draws the attention to the fact, that those parts of the olive (accessory olives), which are apparently connected with the older parts of the cerebellum (vermis), are indeed the most important parts of the olivary complex in lower Vertebrates.

I may add to these remarks that also the fact, found by Holmes and Stewart, that the medial part of the principal olive is connected with the vermis, is in perfect harmony with my results.

It is also clearly shown by Brouwer in his later paper on a second case of cerebellar hemiatrophy, that it is only the most frontal pole of the principal olive and its medial part in the most oral sections, that are connected with the older part of the cerebellum, whereas the rest of the principal olive is in connection with the lateral lobes.

Now these most frontal parts are already present in lowest Mammals, while the caudal and ventro-lateral direction of the development of the principal olive in higher Mammals (chiefly Primates), includes the necessity, that those caudal and ventro-lateral parts are younger.

Indeed it was those olive-parts, that had degenerated when the lesion of the cerebellum was limited to the lateral lobes.

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Just when this article was going to press, I read the paper of George B. Jenkins on the morphology of the sulci and gyri of the olive in Man (A study of the morphology of the Inferior olive — George B. Jenkins — The Anatomical Record, vol 10, N°. 4).

As this author gives an accurate description of the sulci and gyri of the olive in Man, corresponding to the researches of Miss Sabin and Lewis Weed and as my examination refers to the phylogenetic and ontogenetic development of the olive, it will be sufficient to draw the attention to this publication.

As will be clear from my remarks on the accessory olives in this paper, I cannot agree with Jenkins' interpretation of the ventro-medial olive and the intermedial plate.



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STELLINGEN.

I.

De mediale bijolijf is het phylogenetisch oudste gedeelte van het olivaire complex.

II.

De hoofdolijf groeit gedurende de phylogenese caudaalwaarts.

III.

De opvatting der indeeling van het cerebellum in een ouder middens-tuk en phylogenetisch jongere zijgedeelten wordt door de ontwikkelingsgeschiedenis der olijf bevestigd.

IV.

Het is wenschelijk de paraphrenia systematica van Kraepelin naast de paranoia te stellen tegenover de dementia paranoides.

—

V.

Freuds opstelling van algemeen geldige symbolen leidt tot willekeurige droominterpretatie.

VI.

De smaakbekers van het voorste derde gedeelte der tong worden door de nervus facialis geïnnerveerd.

VII.

Men moet ter verklaring der multiple sklerose eene primaire neiging tot gliawoekering aannemen.

VIII.

Het verdient aanbeveling in daarvoor geschikte gevallen van tuberculose, eene tuberculine-behandeling te proberen.

IX.

De opvatting van de decentralisatie der temperatuurregeling volgens Sahli is onjuist.

X.

De hersenpunctie volgens Neisser-Pollack dient niet geheel terzijde gesteld te worden.

XI.

De diagnose eclampsie wordt bemoeilijkt door het feit, dat de graviditeit tot convulsies praedisponeert.

XII.

Ondanks de groote gevaren, die eene trepanatie volgens Elliot door later optredende infectie kan opleveren, moet zij in de behandeling van het glaucoom eene belangrijke plaats innemen.





